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COMPARATIVE AUTECOLOGICAL CHARACTERISTICS OF NORTHWESTERN TREE SPECIES... A LITERATURE REVIEW

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ABSTRACT

This report is a compilation of autecological information previously scattered about in several hundred publications. It includes a comparison of the tolerances, traits, and attributes of native northwestern tree species. The species are ranked with respect to 69 environmental factors, phenotypic characteristics, and physical parameters. These rankings, with the literature references from which they were derived, should be useful aids to species selection, management, and research in the Pacific Northwest.

KEYWORDS: Autecology (plant), native plants, Pacific Northwest.

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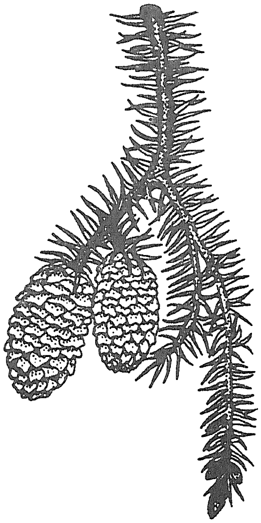

INTRODUCTION

More than 40 native tree species are found in the Pacific Northwest[1] (table 1). Often differing almost as much as do the wide range of environments in which they occur, these species comprise an immensely valuable reservoir of growth traits, physiological tolerances, and physical attributes. By carefully selecting the proper species or combinations of species, foresters and forest researchers can often select biological raw material to fit their management and research needs.

Unfortunately, it is difficult to select biological raw material if one does not have some way of comparing this material in terms of the needs to be filled. Much is known about northwestern tree species, but most of this knowledge is scattered about in numerous publications that often are unavailable or unknown to the foresters and researchers who need them. This report is a collection of such scattered knowledge gleaned from available publications.

Published autecological information was included here whenever references contained comparisons or two or more northwestern tree species. Conclusions obtained by comparing the absolute values resulting from separate observations and experiments have been avoided. As Jarvis (1963) wrote, "The conditions of experiments are never the same as those occurring naturally, so that difficulties arise in applying the results to explain situations observed in the field. However, by doing similar experiments with several species under similar conditions, physiological differences in response between species may be found and these differences may be of ecological significance."

Differences, not absolute values, are presented in this report. Species responses to differing conditions are complex and difficult to compa however, even when only relative differences between species are investigated. Four major problems are involved: (1) Genetic variati within the species being compared may be almost as great as the variation among species, and differing ecotypic responses may obsc species comparisons; (2) Response to differences in one condition may be confounded by responses to differences in other, associated conditions; (3) Species occupying widely diverse environments are difficult to compare directly, and young seedlings often must be grown under artificial conditions if these species are to be compare (4) Young seedlings and older tree do not always respond similarly, a conclusions based upon seedling growth may not be valid for more mature trees. These problems are well summarized by Krajina (1955) and Spurr (1964, p. 165).

Nevertheless, northwestern tree species have been compared by many different investigators in many di ferent environments. If carefully evaluated, these comparisons shoul be useful aids in selecting specie for various environmental conditio When all of them are listed, the published comparisons should also useful indicators of unknown relat ships and research needs.

Although all of the comparisons cited here involve species listed table 1, some of these comparisons did not occur in British Columbia, Washington, Oregon, or Idaho. The were all useful, however, and comparisons that occurred elsewhere w not rejected when species characte istics were evaluated.

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[1] British Columbia, Washington, Oregon, and Idaho.

Scientific name	Common name
abilis (Dougl.) Forbes	Pacific silver fir
ncolor (Gord. and Glend.) Lindl.	White fir
andis (Dougl.) Lindl.	Grand fir
siocarpa (Hook.) Nutt.	Subalpine fir
gnifica A. Murr.	California red fir
gnifica var. *shastensis* Lemm.	Shasta red fir
cera Rehder	Noble fir
ophyllum Pursh	Bigleaf maple
ndo L.	Boxelder
ra Bong.	Red alder
menziesii Pursh	Pacific madrone
apyrifera Marsh.	Paper birch
sis chrysophylla (Dougl.) A.DC.	Golden chinkapin
paris lawsoniana Parl.	Port-Orford-cedar
paris nootkantensis (D. Don) Spach	Alaska-cedar
latifolia Benth.	Oregon ash
s occidentalis Hook.	Western juniper
s scopulorum Sarg.	Rocky mountain juniper
ricina (Du Roi) K. Koch	Tamarack
alli Parl.	Subalpine larch
cidentalis Nutt.	Western larch
us decurrens Torr.	Incense-cedar
pus densiflora (H. and A.) Rehd.	Tanoak
ewveriana Wats.	Brewer spruce
gelmannii Parry ex Engelm.	Engelmann spruce
auca (Moench) Voss	White spruce
riana (Mill.) B.S.P.	Black spruce
tchensis (Bong.) Carr.	Sitka spruce
bicaulis Engelm.	Whitebark pine
tenuata Lemm.	Knobcone pine
ntorta Dougl. ex Loud.	Lodgepole pine
exilis James	Limber pine
ffreyi Grev. and Balf.	Jeffrey pine
mbertiana Dougl.	Sugar pine
nticola Dougl. ex D. Don	Western white pine
nderosa Dougl. ex Loud.	Ponderosa pine
balsamifera L.	Balsam poplar
tremuloides Michx.	Quaking aspen
trichocarpa T. and G. ex Hook.	Black cottonwood
uga menziesii (Mirbel) Franco	Douglas-fir
chrysolepis Liebm.	Canyon live oak
garryana Dougl.	Oregon white oak
kelloggii Newb.	California black oak
sempervirens (D. Don) Endl.	Redwood
evifolia Nutt.	Pacific yew
icata Donn	Western redcedar
terophylla (Raf.) Sarg.	Western hemlock
rtensiana (Bong.) Carr.	Mountain hemlock
aria californica (H. and A.) Nutt.	California-laurel

omenclature is according to Garrison et al. (1976) and Little
For the sake of clarity, scientific names are used throughout
ort.

SHADE TOLERANCE

Shade tolerance will be used here in the restricted sense advocated by Shirley (1943), who defined it as "...the capacity of a tree species to survive in light of low intensity." Proceeding from shade tolerant to intolerant, species are discussed below and ranked in table 2.

Krajina (1965) listed *Abies amabilis* as the most tolerant coniferous tree species in the Pacific Northwest at low elevations and placed it in the same highly tolerant category as *Tsuga mertensiana* and *Chamaecyparis nootkatensis* at subalpine altitudes. Franklin (1964) considered *A. amabilis* to be even more tolerant than *T. mertensiana* in the Washington Cascade Range, also finding it to be more tolerant than *Tsuga heterophylla* in most true fir - hemlock forests. In coastal British Columbia, Schmidt (1957) found *A. amabilis* to at least equal *T. heterophylla* and *Thuja* being the most tolerant of all native coastal conifers. This ranking is supported by Hanzlik (1932), who noted that *A. amabilis* is more tolerant than *Tsuga heterophylla* on the western and southern slopes of the Olympic Mountains. It conflicts with the observations of Buckland et al. (1949), who noted that *A. amabilis* appeared to be less tolerant than *T. heterophylla* on Vancouver Island. Working with the collected observations of others on a national scale, without the local experience of the authorities cited above, Sudworth (1908) and Baker (1949) ranked *Abies amabilis* as less shade tolerant than *Taxus brevifolia, Thuja plicata, Chamaecyparis nootkatensis,* and *Tsuga heterophylla.* Their rankings probably are less accurate than those of Schmidt (1957) Franklin (1964), and Krajina (1965).

The above statements were based upon field observations of seral and climax stands as they existed in nature, where shade tolerance was assumed to have been the dominant

Table 2--Comparative shade tolerance of northwestern tree species[1]

Abies amabilis, Tsuga heterophylla, Taxus brevifolia
Thuja plicata, Chamaecyparis nootkatensis, Tsuga mertensiana
Abies lasiocarpa
Abies grandis
Picea sitchensis
Picea glauca
Abies concolor, Picea breweriana
Abies magnifica var. *shastensis*
Chamaecyparis lawsoniana
Pinus monticola
Pseudotsuga menziesii
Pinus lambertiana
Libocedrus decurrens, Abies procera, Picea engelmannii, Alnus rubra
Pinus contorta
Larix occidentalis
Pinus ponderosa
Juniperus occidentalis, Quercus kelloggii

[1] Compiled from information published by Larsen (1930), Haig et al. (1941), Baker (1949), Buckland et al. (1949), Wood (1955), Edwards (1957), Schmidt (1957), Tackle (1959), Franklin (1964), Franklin and Mitchell (1967), Hodges and Scott (1968), Krajina (1965, 1970), Krueger and Ruth (1969), Thornburgh (1969), Eis (1970), Tinus (1970), Brix (1972), Emmingham and Waring (1973), Franklin and Dyrness (1973), Wali and Krajina (1973), Ronco (1975), Edmonds (1975), Waring et al. (1975). More shade tolerant species are listed above less tolerant ones. Species on the same line are not necessarily equal, but data are insufficient for their separation.

Other factors may have been
d, however, and successional
cannot always be equated
lative shade tolerance. When
ured seedlings growing under
ht conditions, Thornburgh
found *Tsuga heterophylla*
nthesis and height growth
o be higher than those of
nabilis. When all field and
ory observations are con-
, it is difficult to compare
de tolerances of *Abies*
s, Tsuga heterophylla, and
revifolia. Nevertheless,
hree species are the most
olerant trees in the Pacific
st.

a mertensiana is slightly less
t than *Abies amabilis* in
Columbia (Krajina 1970).
(1930) also rated it as
y less tolerant than *Thuja*
and *Taxus brevifolia* in
and northern Idaho--a rating
ed by Baker's nationwide poll
essional opinion in 1949.
ertensiana is the most
t species present at high
ons in most of southern Ore-
anklin 1964), but it may be
ade tolerant than *Abies*
r or *Picea breweriana* in the
u Mountains (Waring et al.

ough Sudworth (1908) noted
amaecyparis nootkatensis is
ade tolerant than *Thuja*
, Krajina (1965, 1970) con-
it to be slightly more
t. Both species probably
ut as shade tolerant as
ertensiana in most environ-
Referring to studies of
g mortality, Harris and Farr
concluded that *Thuja plicata*
shade tolerant than *Tsuga*
hylla or *Picea sitchensis*
heastern Alaska. Their
g mortality may not have
result of shade intolerance,
plicata seems to be less
t in coastal Alaska than it
nd or farther south. Larsen
and Haig et al. (1941) rated
ata as even more shade
t than *Tsuga heterophylla*
Rocky Mountains.

s lasiocarpa is less tolerant
amabilis or *Tsuga mertensiana*
n and Mitchell 1967). De-
e contrary opinions of *Abies lasiocarpa* seems to be considerably more shade tolerant than *Picea engelmannii* (Larsen 1930, Baker 1949, LeBarron and Jemison 1953, Smith and Clark 1960, Krajina 1965). *Abies lasiocarpa* also is more shade tolerant than *Picea glauca, Pinus contorta* (Wali and Krajina 1973), or *Abies grandis* (Larsen 1930, Baker 1949, Schmidt 1957).

Abies grandis seems to be more shade tolerant than *Pseudotsuga menziesii, Pinus monticola,* or *Picea engelmannii* (Sudworth 1908, Larsen 1930, Haig et al. 1941, and Baker 1949). Photosynthetic rates measured by Hodges and Scott (1968) also indicate that it is more shade tolerant than *Abies procera* or *Picea sitchensis.*

Picea sitchensis is more shade tolerant than *Pseudotsuga menziesii* in its native habitat (Wood 1955). *P. sitchensis* also is more shade tolerant than *P. glauca* when grown in controlled environments (Brix 1972).

Although Baker's (1949) poll and Franklin and Dyrness' (1973) tolerance table placed *Picea sitchensis, Abies grandis,* and *A. concolor* in the same "tolerant" category, Krajina's (1965) ranking of *A. concolor* as considerably less tolerant than the other two species probably is correct. *A. concolor* is shade tolerant, however, for Emmingham and Waring (1973) found both *A. concolor* and *A. magnifica* var. *shastensis* at low-light levels where *Pseudotsuga menziesii* was absent in southwest Oregon. Waring et al. (1975) also found the *Abies* species to be more tolerant than *P. menziesii* and observed that *A. concolor* and *Picea breweriana* are slightly more shade tolerant than *A. magnifica* var. *shastensis.*

Abies magnifica var. *shastensis* is more shade tolerant than *Pinus lambertiana* and *P. monticola* (Krajina 1965, Waring et al. 1975). *Pinus lambertiana, P. monticola,* and *Pseudotsuga menziesii* are all given an intermediate tolerance rating by Baker (1949) and Waring et al. (1975); but Krajina (1965) ranked *P. lambertiana* as less tolerant than *Pseudotsuga menziesii, P. monticola* as more tolerant. Krajina's ranking seems more appropriate for environments in which these species occur together.

Chamaecyparis lawsoniana is even more shade tolerant than *Pinus monticola*; and it also ranks above *Pseudotsuga menziesii*, *Pinus lambertiana*, *P. contorta*, *Libocedrus decurrens*, *Abies procera*, *Picea engelmannii*, *Alnus rubra*, and *Larix occidentalis* (Baker 1949, James and Hayes 1954, Franklin and Dyrness 1973). Franklin and Dyrness (1973) place it in the same tolerant category as *Lithocarpus densiflora*, *Acer macrophyllum*, and *Sequoia sempervirens*. Zobel and Hawk[2] found *C. lawsoniana*, *Tsuga heterophylla*, and *Pinus monticola* in the same shady microhabitats.

Hodges and Scott (1968) found that the photosynthetic rate of *Abies procera* was less than that of *Pseudotsuga mensiesii* in low-light conditions, greater than *P. menziesii* in high light. These data support the relative tolerance ratings of Baker (1949), who characterized *P. menziesii* as "intermediate," *A. procera* as "intolerant." They apparently conflict with Krajina's (1970) listing of both *A. magnifica* var. *shastensis* and *A. procera* as more shade tolerant than *P. menziesii*. Interacting light and moisture effects may be responsible for conflicts such as this. Atzet and Waring (1970) found that the minimum light requirement for *P. menziesii* increased where moisture became limiting.

Although Baker (1949) and Franklin and Dyrness (1973) listed *Picea engelmannii* as more tolerant than either *Pseudotsuga menziesii* or *Abies procera*, Tinus' (1970) measurements indicate that *P. englemannii* and *Alnus rubra* probably are less shade tolerant than *P. menziesii*. Where subjective ratings conflict with objective measurements, the measurements have been given precedence here. Tinus' results were used in constructing table 2.

Edmonds (1975), describing the photosynthesis measurements of Helms and Rutter, rated *Libocedrus decurrens* as less tolerant than *Pseudotsuga menziesii*, more tolerant than *Pinus ponderosa*. Again, these measurements conflict with the estimated *Pseudotsuga* - *Libocedrus* ratings compiled by Baker (1949), Krajina (1965), and Franklin and Dyrness (1973); but photosynthetic measurements probably are more reliable than estimates of relative tolerance.

Tinus (1970) and Ronco (1975) measured lower light saturation points for *Picea engelmannii* than for *Pinus contorta*. These measured indications of greater *P. engelmannii* shade tolerance are supported by the conclusions of several observers (Larsen 1930, Haig et al. 1941, Baker 1949, Krajina 1965, and Franklin and Dyrness 1973). The *Pinus contorta* - *Pinus ponderosa* tolerance difference is less distinctive, but *P. contorta* is more shade tolerant than *P. ponderosa* (Larsen 1930, Krajina 1965, Kerr 1913, and Haig et al. 1941).

Although Mosher (1965) implied that *Larix occidentalis* was more shade tolerant than *Pinus contorta* in a northeastern Washington stand, both Baker (1949) and Tackle (1959) considered *L. occidentalis* to be less tolerant. The shade tolerance of *L. occidentalis* has most often been placed somewhere between the tolerances of *Pinus contorta* and *P. ponderosa* (Larsen 1930, Haig et al. 1941, Krajina 1965).

Larsen (1930) and Krajina (1965) considered *Juniperus occidentalis* to be even less shade tolerant than *Pinus ponderosa*. Edwards (1957) also found *Quercus kelloggii* to be less tolerant than *P. ponderosa*. Krajina (1965) listed *Larix lyalli* and *Pinus albicauli* as the most intolerant subalpine specie

LIGHT INTENSITY

Many species comparisons in the literature provide supplementary ligh data in addition to shade tolerance information. Emmingham and Waring (1973 recorded maximum leader growth of *Pseudotsuga menziesii*, *Abies concolor* and *A. magnifica* var. *shastensis* at 100-percent light intensity in southwestern Oregon. Fairbairn and Neustei (1970) noted a similar response for *Picea sitchensis* grown under full sunlight in England but found that *Pseudotsuga menziesii*, *Abies grandis*, and *Tsuga heterophylla* attained maximum height growth at lower light levels. The English environment may have been responsible for this difference.

Controlled environments were utilized by Tinus (1970) in comparing the photosynthesis of several species under increasing light intensities.

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[2] Zobel, Donald B., and Glenn M. Hawk. The environment of *Chamaecyparis lawsoniana*. Unpublished manuscript.

He found that *Picea sitchensis, Tsuga heterophylla,* and *Pseudotsuga menziesii* were light saturated at lower light intensities than *Picea engelmannii* and *Alnus rubra.* Krueger and Ruth (1969) found that *Alnus rubra*'s photosynthetic rate also was higher than those of *Picea sitchensis, Tsuga heterophylla,* and *Pseudotsuga menziesii* at high light intensitities. Clark and Lister (1975) measured three times as much chlorophyll per unit fresh weight in *Alnus rubra* as in *P. menziesii* or *Picea sitchensis* and found *A. rubra* photosynthesis to be more efficient in blue light. The *Alnus rubra* seedling certainly seems to be a marvelously effective photosynthetic mechanism.

Hellmers (1964) measured growth distribution effects in *Sequoia sempervirens* and *Abies magnifica* seedlings grown under different light intensities. Although light intensity scarcely affected growth distribution in *S. sempervirens,* high light intensities produced the greatest basal growth in *A. magnifica.*

When Pharis et al. (1967) made diurnal comparisons of *Pseudotsuga menziesii* and *Pinus ponderosa,* they found that *P. menziesii* photosynthetic rates changed more rapidly than those of *P. ponderosa,* increasing faster in the morning and declining sooner and further in the afternoon.

PHOTOPERIOD

Owston's 1974 observations of the effects of shortened photoperiod indicate that *Picea sitchensis* and coastal *Pseudotsuga menziesii* are more sensitive than *Abies procera* and *Pinus ponderosa* to shortened photoperiods. *Picea sitchensis* seems to have a longer optimum photoperiod than *Thuja plicata* (Malcolm and Caldwell 1971). When Vaartaja (1959) used the ratio of height growth under very long days to height growth under very short days in species comparisons, he found *Picea engelmannii* ≥ *P. sitchensis* ≥ *Pinus contorta* ≥ *P. ponderosa* ≥ *Pseudotsuga menziesii* ≥ *Thuja plicata* ≥ *Tsuga mertensiana.* In general, the more northerly a species, the greater was its photoperiodic sensitivity.

TEMPERATURE

Genetic variation within species often makes the comparison of species temperature responses difficult. Different geographic races of the same species differ--sometimes in unexpected ways. For example, northern races and those from inland locations usually are more frost tolerant than their southern and coastal relatives (Haller 1961) Sakai and Okada 1971, Sakai and Weiser 1973). Nevertheless, Conkle et al. (1967) observed more winter injury in *Abies concolor* seedlings from northern locations than in those from southern seed sources. Within-species variation should be kept in mind when pondering the species comparisons presented here. Species temperature responses are considered under three categories: frost tolerance, heat tolerance, and mean temperature conditions.

FROST TOLERANCE

Frost tolerance comparisons are most abundant in the literature. They are summarized in table 3.

The freezing resistances of dormant buds and twigs measured by Sakai and Weiser (1973) show that *Pinus contorta* and *Pinus monticola* are the most frost-resistant northwestern tree species while in the dormant state. Their data indicate *Picea engelmannii* to be the next most resistant, followed by *Populus trichocarpa, Alnus rubra, Abies lasiocarpa* and *A. concolor, Larix occidentalis, Pinus ponderosa, P. jeffreyi, Picea sitchensis, Chamaecyparis nootkatensis, Thuja plicata* and *Abies grandis, A. amabilis, Pseudotsuga menziesii, Tsuga mertenziana,* and *T. heterophylla*...in approximately that order. This frost resistance ranking, derived from the comparison of frost damage to dormant twigs artificially hardened before freezing in the laboratory, somewhat resembles the less complete but more realistic ranking that can be created by compiling literature references to frost damage in actively growing trees.

Table 3--Comparative frost tolerances of northwestern tree species[1/]

Pinus contorta, P. monticola
Picea engelmannii
Populus trichocarpa
Pinus ponderosa, P. jeffreyi, Abies magnifica var. *shastensis, Tsuga mertensiana*
Libocedrus decurrens, Picea breweriana
Pinus lambertiana
Abies concolor, A. lasiocarpa
Abies grandis, A. amabilis
Picea sitchensis
Pseudotsuga menziesii
Thuja plicata
Tsuga heterophylla
Arbutus menziesii

[1/] Compiled from information published by Day (1928), Schubert (1955), Duffield (1956), Daubenmire (1957), Wagener (1960), Haller (1961), Stein (1963), Fowells and Stark (1965), Krajina (1970), Cochran and Berntsen (1973), Sakai and Weiser (1973), Waring et al. (1975), and Timmis (undated). Tolerant species are listed above intolerant ones. Species in the same group are not necessarily equal, but data are insufficient for their separation.

Young *Pinus contorta* seedlings are more frost tolerant than young *P. ponderosa* seedlings (Berntsen 1967, Cochran and Berntsen 1973), and a late spring frost in central Oregon damaged *P. contorta* megasporangiate strobili much less than *P. ponderosa* strobili at the same stage of development (Sorensen and Miles 1974).

Pinus jeffreyi may be slightly more frost tolerant than *P. ponderosa* near the California coast (Haller 1959, 1961), but the two species appear equally frost tolerant elsewhere (Wagener 1960, Haller 1961). Frost tolerances of *Abies magnifica* var. *shastensis* and *Tsuga mertensiana* equal that of *P. jeffreyi* (Waring et al. 1975).

Waring et al. noted that *Picea breweriana* is less tolerant of cold temperatures than *Pinus jeffreyi*, more tolerant than *Abies grandis, Pseudotsuga menziesii*, or *Pinus jeffreyi*. As *Libocedrus decurrens* is less frost tolerant than *Pinus ponderosa* but more tolerant than *Abies grandis, Pseudotsuga menziesii*, or *Pinus lambertiana* (Stein 1963, Fowells and Stark 1965), it may be ranked with *Picea breweriana* in this respect.

Schubert (1955) observed that *Pinus lambertiana* was more susceptible to freezing than *P. ponderosa* and *P. jeffreyi*. *P. lambertiana* survival also was poorer than *Libocedrus decurrens* survival, but better than that of *Abies concolor* in the frost mortality measurements made by Fowells and Stark (1965) in California. Stein's (1963) southwestern Oregon observations were similar--frost damage to *Pinus lambertiana* was more severe than to *Libocedrus decurrens*, but less severe than that to *Abies grandis* or *Pseudotsuga menziesii*. *P. menziesii* is less frost tolerant than *Picea glauca* in the interior of British Columbia (Cayford and Bickerstaff 1968).

A November 1955 cold wave in western Washington damaged the *Abies* spp. less than *Picea sitchensis*, and *P. sitchensis* was less damaged than *Pseudotsuga menziesii* (Duffield 1956). Day (1928) also found *Picea sitchensis* to be more frost resistant than *Pseudotsuga menziesii* in England. Sakai and Okada (1971) found the dormant frost resistance of *Picea sitchensis* to be similar to that of *Chamaecyparis lawsoniana*, but Duffield (1956) observed more damage to *C. lawsoniana* than to *P. sitchensis* after the November freeze. Similarly, the excellent dormant frost tolerance of *Alnus rubra* reported by Sakai and Weiser (1973) was not evident in November, 1955, when *Alnus* and *Arbutus* trees were extensively killed by unusually cold temperatures (Daubenmire 1957). As Sakai and Weiser measured only the frost tolerance of detached dormant twigs, Duffield's and Daubenmire's observations of entire trees probably are more pertinent. Both Duffield (1956) and Daubenmire (1957) found *Pseudotsuga menziesii* more frost tolerant than *Thuja plicata*, and *T. plicata* more tolerant than *Tsuga heterophylla*. These observations apply only to the shoots, however, for Van Eerden (1974) found *Pseudotsuga* roots to be more susceptible to low temperatures than *Tsuga* roots. *Arbutus menziesii* is "...the least frost resistant tree native to Canada" (Krajina 1970).

HEAT TOLERANCE

Levitt (1951) stated that frost, heat, and drought resistances are basically similar, with resistance to one accompanied by resistance to the other two factors. Although this seems to be true in a general sense, relative resistances to heat injury are not the same as resistances to frost injury when species rankings from the literature are compiled and compared. Unfortunately, only a few species have been compared for heat tolerance.

Pinus lambertiana is more heat resistant than *P. ponderosa* or *Pseudotsuga menziesii* (Cochran 1963). The heat tolerance of *Pinus jeffreyi* is at least equal to that of *P. ponderosa* (Haller 1959), but no *P. jeffreyi* - *P. lambertiana* comparisons are available. *Pseudotsuga menziesii*, *Pinus monticola*, and *Larix occidentalis* seedlings are more heat resistant than *Tsuga heterophylla* or *Thuja plicata* seedlings (Haig 1936). *Pseudotsuga* seedlings also are more resistant than those of *Abies grandis* (Baker 1929), which is more susceptible to heat killing than other species (Schubert and Adams 1971). *Abies lasiocarpa* is able to establish itself in hotte conditions than *Picea engelmannii* *p. glauca* hybrids in the Rocky Mountains (Day 1964).

MEAN TEMPERATURE CONDITIONS

In addition to comparing frost and heat responses, it often is advantageous to compare species responses to mean temperatures. This may be done by comparing the published relative occurrence and/ growth of species observed under identical temperatures...for seve different temperature conditions.

Quercus kelloggii, *Quercus gar ana*, and *Arbutus menziesii* occur i the warmest northwestern environments (Cleary and Waring 1969, Zob et al. 1976). In the eastern Sisk you Mountains of southern Oregon, *Pinus ponderosa* also often occurs in hot environments (Waring 1969).

Frost tolerance notwithstanding *Pinus contorta* does not seem to grow any better than *P. ponderosa* under low night temperatures (Cochran 1972). Its boreal range extends farther north, however, than that of *P. ponderosa* (Harlow and Harrar 1950). Although it demands a lower average temperatur than *P. ponderosa* and *Pseudotsuga menziesii* in the Rocky Mountains, *Pinus contorta* probably requires a higher temperature than *Picea engelmannii* or *Abies lasiocarpa* (Tackle 1959). Kaufmann and Eckar (1977) recently suggested that *Picea engelmannii* establishment may occur more rapidly than that o *Pinus contorta* in cool environment

In the central Oregon Cascades *Pseudotsuga menziesii*, *Pinus lambertiana*, *Acer macrophyllum*, and *Libocedrus decurrens* are most important where environments are slightly cooler than those typical of *Arbutus*'s center of importance (Zobel et al. 1976). In controlled environments, *Pseudotsuga menziesii* grows less well than *Pinus ponderosa* under high tempera conditions (see Steinbrenner and Rediske 1964, Pharis et al. 1967). Nevertheless, high temperatures se to be less detrimental to *P. menziesii* than they are to *Tsuga heterophylla* (Brix 1971). A small diurnal temperature variation appears to be beneficial for *P. menziesii*, but variation is not required for *Sequoia sempervirens* (Hellmers and Sundahl 1959).

When Oregon Cascade environments cooler than those typical of *Pseudotsuga menziesii*-dominated stands are considered, *Thuja plicata, Tsuga heterophylla, Abies grandis, A. procera,* and *A. amabilis* become more important as temperatures drop (Zobel et al. 1976). *Abies magnifica* var. *shastensis* and *Tsuga mertensiana* occupy the coolest forested environments in the eastern Siskiyou Mountains (Cleary and Waring 1969).

Farther north, timberline for *Abies amabilis* in British Columbia is about 150 m (492 ft) lower than timberline for *Tsuga mertensiana, Abies lasiocarpa,* and *Pinus albicaulis* (Krajina 1970). Using controlled temperatures, Brix (1972) found *Picea glauca* to be more productive than *P. sitchensis* under high temperature - high light conditions.

A complete ranking of the mean temperature relations of northwestern tree species has not been attempted, but approximate relationships based upon available information are summarized in table 4. The approximate accuracy of field observation is associated with a Rocky Mountain ranking of species susceptibility to "red belt" injury (Mason 1915):

Juniperus sp. (most resistant)
Abies lasiocarpa
Picea engelmannii
Pinus contorta
Pseudotsuga menziesii
Pinus ponderosa (least resistant)

Red belt injury apparently results from crown desiccation that occurs when high needle transpiration is accompanied by frozen ground conditions that prevent water uptake. As such, it is a combination of temperature and moisture phenomena.

MOISTURE

Moisture comparisons among species may be considered in three categories: tolerance of deficient moisture, tolerance of excess moisture, and optimum moisture conditions. If quantity of published information is any indication of the relative importance of these categories, ability to endure deficient moisture (drought tolerance) is most important.

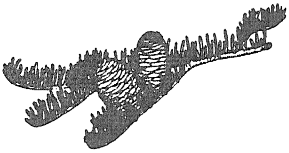

Table 4--Mean temperature relationships among northwestern tree species[1]

Pinus ponderosa, Quercus kelloggii, Quercus garryana, Arbutus menziesii
Pseudotsuga menziesii, Pinus lambertiana, Libocedrus decurrens, Acer macrophyllum
Thuja plicata
Tsuga heterophylla
Abies grandis
Abies amabilis, A. procera, A magnifica var. *shastensis*
Tsuga mertensiana, Abies lasiocarpa, Pinus albicaulis
Pinus contorta
Picea mariana, P. glauca, Larix laricina

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[1] Compiled from information published by Hustich (1953), Steinbrenner and Rediske (1964), Pharis et al. (1967), Waring (1969), Cleary and Waring (1969), Krajina (1970), Brix (1971), and Zobel et al. (1976). Species adapted to warm temperatures are listed above those adapted to cool temperatures. Species in the same group are not necessarily equal, but data are insufficient for their separation.

DROUGHT TOLERANCE

Dry conditions may be endured by trees; or they may be avoided (by rapid and deep root growth, for example). In either case, several physiological attributes contribute to drought tolerance. Unfortunately, related attributes do not always coincide with overall tolerance and different researchers do not always agree. This is particularly true of the drought endurance associated with stomatal closure. Hodges (1967) found that *Abies procera* stomata closed more completely than *Pseudotsuga menziesii* stomata at night...and *P. menziesii* stomata closed more completely than *Tsuga heterophylla* and *Picea sitchensis*. *Abies concolor* stomata did not close at all. Hodges and Scott (1968) concluded that *A. procera* controlled internal moisture better than the other species. Running (1973, 1976) noted that *A. procera* showed little stomatal control, however, whereas *Pseudotsuga menziesii* and *A. concolor* appeared to have good control. When the data and conclusions of different researchers differ so, it is difficult to integrate them. In this case, characteristics of the environments in which the species normally occur make Running's conclusions seem more appropriate than those of Hodges and Scott.

Lopushinsky (1969) also studied stomatal closure. He found that *Pinus ponderosa*, *P. contorta*, and *Picea engelmannii* stomata closed sooner than those of *Pseudotsuga menziesii* and *Abies grandis*. Wambolt (1973), in a study of conifer water potential, concurred with Lopushinsky in ranking *Pinus ponderosa* stomatal control as more sensitive than that of *P. contorta*, *Picea engelmannii*, and *Pseudotsuga menziesii*.

Barker (1973) observed less stomatal control in *Abies concolor* than in *Pinus ponderosa* under comparable environmental conditions, but Rutter (1977), working with foliar samples exposed to full sunlight in the field, recorded more stomatal control in *A. concolor*. He found *Libocedrus decurrens* stomata to be more sensitive to increasing moisture stress than those of *A. concolor* or *P. ponderosa* and attributed its drought tolerance to stomatal control, suggesting that the long tap root of *P. ponderosa* allows it to avoid moisture stress rather than tolerate it. Rutter worked with day-to-day fluctuations that resulted in few common environmental conditions for the three species studied, however; and he did not attempt to account for within tree, between tree, or seasonal differences in behavior. Perhaps these unmeasured variables affect Rutter's *Pinus ponderosa* observations. Cleary (1971) observed an abrupt decline in *P. ponderosa* photosynthesis at moderate plant moisture stress (15-20 atm), a gradual decline in *Pseudotsuga menziesii* photosynthesis over a much wider range (<8->22 atm). Both declines probably were associated with stomatal closure.

Stomatal closure has not been studied in all northwestern tree species, but drought tolerance as such has been widely studied and observed (table 5). This may be just as well, for as Parker (1969) observed, whole seedlings involve other adaptations that may be more important than leaf resistance alone.

Franklin and Dyrness (1973) ranked *Quercus garryana* as the most moisture-stress tolerant southwestern Oregon major tree species, followed by *Quercus kelloggii*, *Pinus ponderosa*, and *Arbutus menziesii*. They did not rank *P. jeffreyi*, but Stone (1957), studying the effect of artificial dew on the survival of four western conifers, observed that unwatered seedlings of *P. jeffreyi* in greenhouse cans survived longer than unwatered *P. ponderosa*, *Libocedrus decurrens*, or *Abies concolor* seedlings. When he applied artificial dew in the form of a nightly water spray, *A. concolor* still died first, followed by the pines (together) and finally *L. decurrens*. Stone qualified his results by pointing out that greenhouse behavior may not duplicate that in the field, where differences in relative root growth rates among species might alter the relative drought resistance observed in greenhouse containers. Nevertheless, Haller (1959) noted that *Pinus jeffreyi* is more tolerant of aridity

Table 5--Comparative drought tolerances of northwestern tree species[1]

Quercus garryana
Quercus kelloggii
Pinus jeffreyi
Pinus ponderosa
Pinus contorta, Libocedrus decurrens, Arbutus menziesii
Pseudotsuga menziesii
Picea engelmannii
Abies grandis
Pinus lambertiana, Larix occidentalis
Abies lasiocarpa, Thuja plicata, Pinus monticola
Abies concolor, Picea breweriana
Chamaecyparis lawsoniana
Tsuga heterophylla, Picea sitchensis
Abies amabilis
Abies magnifica var. *shastensis, Tsuga mertensiana*

[1] Compiled from information published by Daubenmire (1943), Tarrant (1953), Stone (1957), Haller (1959), Cochran (1963), Pharis (1966), Fraser and Cordes (1967), Kotar (1972), Franklin and Dyrness (1973), and Edmonds (1975). Drought tolerant species are listed above intolerant ones. Where species occur on the same line, information is insufficient to separate them.

than *P. ponderosa* in California. Tarrant (1953), comparing the characteristics of *P. ponderosa* and *P. contorta* in a literature review, attributed more drought tolerance to *P. ponderosa*. *P. ponderosa* also has a greater physiological capacity to exploit hot, dry environmental conditions than *L. decurrens* (Edmonds 1975) or *Pseudotsuga menziesii* (Daubenmire 1943, Daubenmire and Deters 1947, Parker 1951, and Cochran 1963).

Further comparisons involving *P. menziesii* are numerous. Marshall (1931), measuring critical soil moisture and survival, observed that *P. menziesii, Abies grandis,* and *Thuja plicata* survived with less soil moisture than that required by *Pinus monticola, Tsuga heterophylla,* or *Picea glauca.* Although transpiration rates declined faster in *Picea engelmannii* than in *Pseudotsuga menziesii* and *Abies grandis* when potted seedlings were subjected to moderate soil moisture stresses by Lopushinsky and Klock (1974), Daubenmire (1943) observed that *Pseudotsuga menziesii* survived longer than *Picea engelmannii* and *P. engelmannii* survived longer than *Abies lasiocarpa* or *Thuja plicata* when his potted seedlings were maintained at or below the wilting point for 2, 4, 6, 8, and 10 days. Using diurnal variations in sap pressure and dormancy as their criteria. Fraser and Cordes (1967) rated *Pseudotsuga menziesii* more able to avoid moisture stress than *Tsuga heterophylla* or *Picea sitchensis*.

When Parker (1951) cut leaves from several tree species and measured moisture retention, *Pseudotsuga menziesii* leaves retained a higher moisture content than those of *Picea engelmanni, Thuja plicata, Abies grandis,* or *Pinus monticola.* Measuring foliage moisture content and soil moisture stress, Pharis (1966) ranked *Pseudotsuga menziesii* and *Libocedrus decurrens* above *A. grandis and A. grandis* above *Pinus lambertiana* in drought resistance. In considering these comparisons, it is important to remember that *P. menziesii* trees from different geographic localities... and even from different aspects... may differ in drought resistance (Pharis and Ferrell 1966, Ferrell and Woodward 1966). Similar variation probably occurs in other species.

Pinus lambertiana seems to be more drought tolerant than *P. monticola* in southwestern Oregon

(Franklin and Dyrness 1973); and *P. monticola* appears to be less able to adapt to inadequate soil moisture than *Pseudotsuga menziesii*, *Abies grandis*, *Larix occidentalis*, or *Thuja plicata* in the western white pine type (Leaphart and Wicker 1966). Southwestern Oregon *Pinus lambertiana* also is more drought tolerant than *Picea breweriana*, which is quite tolerant of soil moisture stress but intolerant of evaporative demand (Waring et al. 1975). Waring et al. indicate that *Abies concolor* in southwestern Oregon slightly exceeds *P. breweriana* in ability to tolerate evaporative demand but is a little less tolerant of soil moisture stress. *Tsuga mertensiana* and *Abies magnifica* var. *shastensis* are much less tolerant of soil moisture deficiencies.

Franklin and Dyrness (1973) ranked *Chamaecyparis lawsoniana*, *Abies magnifica* var. *shastensis*, *Tsuga mertensiana*, and *T. heterophylla* below *Abies concolor* in decreasing order of moisture stress tolerance in southwestern Oregon. As Kotar (1972) found *T. heterophylla* to be more drought tolerant than *Abies amabilis* when seedlings of both species were subjected to high moisture stresses in the laboratory and as Lowry's 1972 laboratory measurements showed *A. amabilis* to be more drought tolerant than *Tsuga mertensiana*, Franklin and Dyrness's *Tsuga* rankings probably should be reversed. *Tsuga heterophylla* seems to be more drought tolerant than *T. mertensiana*. Puritch (1973) in comparing the effect of water stress on photosynthesis, respiration, and transpiration of four *Abies* species, found *A. grandis* to be most stress tolerant, followed by *A. lasiocarpa*, *A. amabilis*, and *A. balsamea*--in that order.

EXCESS MOISTURE

Excess moisture usually is the result of flooding or the presence of a shallow water table in nature. Observations of flood mortality, through sometimes confounded by other factors, often provide the only available species comparisons. Brink (1954), observing the results of a 1948 spring flood in the lower Fraser River Valley, found *Picea sitchensis*, *Pinus contorta*, and *Thuja plicata* mortality to be lower than that of *Tsuga heterophylla*. *T. heterophylla* mortality was lower than that of *Pseudotsuga menziesii* or *Alnus rubra*. Krajina (1970) observed that *Populus trichocarpa*, *P. tremuloides*, *Abies grandis*, *A. lasiocarpa*, *Thuja plicata*, *Picea sitchensis*, *P. engelmannii*, *P. glauca*, and *Tsuga heterophylla* survive on floodplain habitats where *Pseudotsuga menziesii* cannot grow. *Sequoia sempervirens* and *Umbellularia californica* survive flooding that kills *P. menziesii*, *A. grandis*, and *Lithocarpus densiflora* (Stone and Vasey 1968).

Controlled flooding experiments indicate that *Pinus contorta* is more tolerant of oxygen deficiency than is *Picea sitchensis* (Boggie 1974, Crawford and Baines 1977), surviving better when seedlings of both species are artificially flooded (Minore (1968). Minore also found *Pinus contorta* and *Thuja plicata* seedlings to be more flood tolerant than those of *Alnus rubra* and *Tsuga heterophylla*, which were more tolerant than *Pseudotsuga menziesii* seedlings. Gill (1970), however, emphasized in his excellent flooding review that it probably is not permissible to extrapolate from seedling performance to mature trees when dealing with flood tolerance. Physical size may be very important.

Soil characteristics apparently influence species tolerance of shallow water tables in nature. Howell (1931) found *Pinus contorta* in the saturated soil over hard pan areas in California and claimed that *P. ponderosa* could not endure such excess moisture. Like Howell, Tarrant (1953) concluded that *P. contorta* was very tolerant of continuous high soil moisture but *P. ponderosa* was intolerant. In contrast, Stephens (1965) observed that *P. ponderosa* thrived on imperfectly drained soils with clay subsoils developed from Eocene to Miocene volcanic rocks in the western Cascade Mountains of Oregon, growing better than *Pseudotsuga menziesii* or *Pinus lambertiana* on these moist, fine-textured substrates. The Eocene to Miocene parent materials seem to be uniquely effective in favoring *P. ponderosa* on wet sites. More than moisture must be involved, for Cochran (1972) obtained no significant mortality in either *P. ponderosa* or *P. contorta* when he subjected seedlings to carefully controlled shallow water-table conditions in a greenhouse. Haller (1959) indicated that *P. jeffreyi* is at least as tolerant of high moisture as *P. ponderosa.*

Minore and Smith (1971), reporting on the occurrence and growth of four tree species in swamps and stream bottoms on the Olympic Peninsula, ranked *Alnus rubra* and *Thuja plicata* as most tolerant of shallow water tables, followed by *Picea sitchensis* and (least tolerant) *Tsuga heterophylla.* Absence of *Pseudotsuga menziesii* in these wet habitats indicated even less tolerance than *T. heterophylla.* When Minore (1970) compared the seedling growth of eight species over artificial water tables, he found *Pinus contorta, Thuja plicata, Alnus rubra,* and *Picea sitchensis* to be more tolerant of shallow water tables than *Pseudotsuga menziesii.* These and other excess-moisture tolerance relationships are summarized in table 6.

OPTIMUM MOISTURE

Optimum moisture conditions are difficult to determine in controlled growthchamber or greenhouse environments. Other environmental factors influence species growth, and the resulting interactions often are difficult to identify and analyze. Where optimum conditions are defined on the basis of natural range comparisons in the field, further difficulties arise. Competition from other species may influence the species range under consideration, and the observed moisture range may not be the optimum range. Nevertheless, the results of controlled-environment experiments where moisture conditions for the maximum growth of two or more species are compared would provide useful information, and species occurrences along moisture gradients in nature probably reflect their moisture optima in a relative sense.

Controlled-environment experiments involving moisture conditions for maximum growth seem to be almost non-existent. Steinbrenner and Rediske (1964), however, did find that *Pseudotsuga menziesii* seedlings were more responsive to high levels of moisture and humidity than *Pinus ponderosa* seedlings.

A few investigators have observed species presence along measured moisture gradients in the field. Waring and Major (1964) ranked 10 northwestern species in coastal northern California by assigning "ecological optimum" numbers along a scale of 0 (dry) to 100 (wet): *Libocedrus decurrens* (on serpentine soil)--0, *Quercus kelloggii* and *Q. garryana*--10, *Pseudotsuga menziesii*--

Table 6--Comparative tolerances of northwestern tree species to excess moisture[1]

Pinus contorta, Thuja plicata, Tsuga mertensiana, Chamaecyparis nootkatensis, Abies lasiocarpa, Sequoia sempervirens, Populus trichocarpa, Umbellularia californica
Alnus rubra
Pinus ponderosa, P. jeffreyi, Picea sitchensis, Abies grandis
Tsuga heterophylla
Pseudotsuga menziesii

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[1] Compiled from information published by Howell (1931), Brink (1954), Wood (1955), Haller (1959), Stone and Vasey (1968), Minore (1968, 1970), Krajina (1970), Minore and Smith (1971), Boggie (1974), and Crawford and Baines (1977). Moisture tolerant species are listed above intolerant ones. Where species occur in the same

17, *Arbutus menziesii*--20, *Lithocarpus densiflora*--25, *Sequoia sempervirens*--62, *Alnus rubra*--78, *Acer macrophyllum*--85, and *Populus trichocarpa*--100. Waring (1969) also positioned major forest vegetation types of the eastern Siskiyou Mountains of southwestern Oregon along a gradient from dry (*Quercus kelloggii*) to wet (*Abies magnifica* var. *shastensis* and *Tsuga mertensiana*). Farther north, in the central western Cascade Range of Oregon, Zobel, et al. (1976) ranked tree species distribution along a plant moisture stress gradient. In order, the species are: *Arbutus menziesii* (dry), *Libocedrus decurrens* and *Pinus lambertiana*, *Acer macrophyllum* and *Pseudotsuga menziesii*, *Tsuga heterophylla* and *Thuja plicata*, *Abies grandis*, *Abies procera* and *A. amabilis*, and *Tsuga mertensiana* (wet).

Most comparisons of optimum moisture conditions among northwestern tree species consist of somewhat subjective statements based upon careful observation and field experience. Species that grow in moist conditions often are compared to *Pseudotsuga menziesii* in these statements. For example, *Tsuga heterophylla*, *Thuja plicata*, *Abies procera*, *A. amabilis*, and *Picea sitchensis* all require more moisture than *Pseudotsuga menziesii* (see Munger 1940, Forest Soils Committee of the Douglas-fir Region 1957, and Aller 1956). Comparisons among two or three species provide more detail and help to refine these rather broad contrasts. They have been combined whenever possible and summarized in table 7.

Day (1957) suggested that *Thuja plicata* requires more moisture than *Picea sitchensis* or *Tsuga heterophylla*. Habeck (1968) observed *T. heterophylla* dominating *Thuja plicata* on well-drained slopes, *T. plicata* dominating *T. heterophylla* on poorly drained depressions and wet ravines in Glacier National Park. Wood (1955) noted that *Picea sitchensis* dominated *T. heterophylla* on moist sites but not on dry ones in southeastern Alaska. Combining the observations of these three authors, one can rank the three species in order: *Thuja plicata* (very moist), *Picea sitchensis*, and *Tsuga heterophylla* (less moist). Furthermore, the information presented by Zobel et al. (1976) indicates that *Thuja plicata* prefers slightly drier habitats than *Tsuga mertensiana*, *Abies amabilis*, and *A. procera*. Zobel and Hawk's (see footnote 2, page 5) observations suggest that

Table 7--Optimum moisture relationships among northwestern tree species[1]

Tsuga mertensiana, *Abies amabilis*, *A. procera*, *A. magnifica* var. *shastensis*, *A. concolor*, *Populus trichocarpa*
Abies grandis
Thuja plicata
Picea sitchensis
Tsuga heterophylla
Acer macrophyllum
Alnus rubra
Pseudotsuga menziesii
Pinus ponderosa
Pinus lambertiana, *Libocedrus decurrens*
Arbutus menziesii
Quercus garryana, *Quercus kelloggii*

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[1] Compiled from information published by Munger (1940), Wood (1955), Day (1957), Forest Soils Committee (1957), Steinbrenner and Rediske (1964), Thilenius (1964), Aller (1956), Habeck (1968), Newton et al. (1968), Waring and Major (1964), and Zobel et al. (1976). Species with moist optimums are listed above those with

Chamaecyparis lawsoniana may require more moisture than *Pseudotsuga menziesii*. Combining and comparing observations made in different areas in this way introduces an unknown amount of ecotypic variation, but species comparisons often are not possible otherwise.

Abies lasiocarpa requires moister habitats than *Picea engelmannii* (Smith and Clark 1960, Krajina 1970) or *Pinus contorta* (Wali and Krajina 1973). Further examination of the literature indicates that *P. engelmannii* requires more moisture than *P. contorta*, and *P. contorta* requires more moisture than *Pseudotsuga menziesii* or *Pinus ponderosa* (Tackle 1959). *Pinus contorta* requires less drainage than *P. ponderosa* (Kerr 1913), and it makes better growth than *P. ponderosa* on wet sites (Youngberg and Dyrness 1959). Unfortunately, information relating *Pinus contorta*, *Abies lasiocarpa*, and *Picea engelmannii* to other species is lacking.

Some information is available for northwestern hardwoods. According to the previously cited ecological optima of Waring and Major (1964), *Acer macrophyllum* prefers slightly more moisture than *Alnus rubra*. Both of these species appear to be suited to slightly more moist sites than *Pseudotsuga menziesii* (Thilenius 1964, Newton et al. 1968). *Lithocarpus densiflora* requires more moisture than *Arbutus menziesii*, *Quercus garryana*, or *Q. kelloggii* (Roy 1962).

NUTRIENTS

MACRONUTRIENT CONCENTRATIONS

Relative foliage, wood, bark, and litter concentrations of the mineral elements necessary for plant growth apparently differ among northwestern tree species. These concentrations vary somewhat with soils and season, so concentration differences may or may not reflect relative species nutrient requirements. Nevertheless, they do influence the environments in which they occur. Different species contribute differing kinds and quantities of nutrient material to their surroundings. Some of these difference have been extracted from the literature and ranked as relative macronutrient concentrations in table 8.

Working on several soils, Daubenmire (1953) measured the nutrient content of freshly fallen foliage from 12 northern Rocky Mountain species--species that also occur in the Pacific Northwest. He suggested that the high calcium content of *Thuja plicata* litter was at least partly responsible for the higher pH of soil measured under this species. Surprisingly, the even higher calcium content of *Abies grandis* litter produced no such effect. Alban (1969) measured higher soil pH, exchangeable calcium, cation-exchange capacity, base saturation, and organic matter under old *Thuja plicata* than under old *Tsuga heterophylla* trees.

Tarrant et al. (1951) also worked on several soils when they measured nutrients in the annual litter fall of 10 northwestern tree species, but Webber (1973) studied young trees on a single soil type. He measured higher calcium contents in *Thuja plicata* than in either *Tsuga heterophylla* or *Pseudotsuga menziesii*. Webber's data, like those recorded for young seedlings by Lavender (1962) but unlike the information published by Tarrant et al. (1951), Daubenmire (1953), and Ovington (1956), show *Tsuga heterophylla* to have more calcium than *Pseudotsuga menziesii*. Soil diversity and ages of the trees, foliage, and litter sampled may be responsible for these differences. When mature trees are analyzed, calcium concentrations seem to be higher in *Pseudotsuga menziesii* than in *Tsuga heterophylla*.

Regardless of soil or age, there seems to be little doubt of the high calcium characteristic of *Thuja plicata*. Beaton, Moss et al. (1965) found calcium content to be higher in *T. plicata* foliage than in the foliage of forest grown *Abies lasiocarpa*, *A. amabilis*, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Picea sitchensis*, or *P. engelmannii*; and Ovington (1956) found both *Thuja plicata* and *Chamaecyparis lawsoniana* leaves to be richer in calcium than those of *Pseudotsuga menziesii* or *Tsuga heterophylla*. The *Thuja* and *Chamaecyparis* leaves and litter layers also had higher

Table 8--Relative macronutrient concentrations in northwestern tree species[1/]

Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	Sulfur
Alnus rubra	*Larix occidentalis*	*Populus tremuloides*	*Abies grandis*	*Picea sitchensis*	*Pseudotsuga menziesii*
Abies amabilis	*Populus tremuloides*	*Acer macrophyllum*	*Populus tremuloides*	*Pinus ponderosa, P. contorta, P. monticola*	*Tsuga heterophylla*
Picea sitchensis	*Pseudotsuga menziesii*	*Alnus rubra*	*Thuja plicata, Abies amabilis*	*Abies amabilis, Tsuga heterophylla*	*Thuja plicata*
Acer macrophyllum	*Alnus rubra, Tsuga heterophylla, Abies lasiocarpa*	*Pinus ponderosa*	*Acer macrophyllum*	*Thuja plicata*	
Pinus contorta	*Abies amabilis, Pinus ponderosa, P. monticola, P. albicaulis, Abies grandis, Picea engelmannii, Acer macrophyllum*	*Pseudotsuga menziesii, Larix occidentalis*	*Pseudotsuga menziesii*	*Pseudotsuga menziesii*	
Populus tremuloides	*Picea sitchensis*	*Abies grandis*	*Picea engelmannii*	*Acer macrophyllum*	
Abies lasiocarpa	*Thuja plicata*	*Thjua plicata*	*Abies lasiocarpa*	*Alnus rubra*	
Abies grandis	*Pinus contorta*	*Pinus contorta*	*Abies amabilis*		
Pseudotsuga menziesii		*Tsuga heterophylla*	*Alnus rubra*		
Picea engelmannii		*Abies magnifica* var. *shastensis, Picea engelmannii*	*Pinus monticola*		
Pinus ponderosa		*Pinus monticola*	*Pinus contorta, Tsuga heterophylla*		
Tsuga heterophylla		*Abies amabilis, Picea sitchensis*	*Picea sitchensis*		
Pinus albicaulis		*Pinus albicaulis*	*Larix occidentalis*		
Larix occidentalis			*Pinus ponderosa*		
Thuja plicata			*Pinus albicaulis*		

[1/] Compiled from foliage, wood, bark, and litter data published by Tarrant et al. (1951), Daubenmire (1953), Ovington (1956), Wollum and Youngberg (1964), Beaton, Moss et al. (1965), van den Driessche (1969 and Webber (1973). Species are ranked from high concentration (top) to low concentration (bottom) in the lists. Species in the same group are not necessarily equal, but data are insufficient for species comparisons within groups.

pH values. *Chamaecyparis lawsoniana* leaf nutrient concentrations are similar to those found in *Thuja plicata*, except for higher magnesium (Zobel and Hawk undated).

Although *Thuja plicata* sapwood has more calcium than *Pseudotsuga menziesii*, it does not differ significantly from *Tsuga heterophylla* or *Alnus rubra* with respect to sapwood calcium content (Radwan 1969). Radwan's data show that *A. rubra* sapwood has more nitrogen and magnesium, but less iron than that of *Thuja plicata*, *Tsuga heterophylla*, or *Pseudotsuga menziesii*. Relative sapwood and foliage concentrations probably differ when species are compared, for the data of Tarrant et al. (1951) show *A. rubra* foliage to have less magnesium than other species.

Tarrant et al. (1951), Daubenmire (1953), and Wollum and Youngberg (1964) all found *Pinus ponderosa* litter to be lower than *Pseudotsuga menziesii* litter in calcium and nitrogen contents. *Thuja plicata* also ranked below *P. menziesii* with respect to nitrogen concentration. Indeed, published data indicate that *T. plicata* may have the lowest nitrogen content of any northwestern tree species (Tarrant et al. 1951, Daubenmire 1953, Beaton, Moss et al. 1965, and Webber 1973). In contrast, *Alnus rubra* may be top ranked for nitrogen content (Tarrant et al. 1951, Wollum and Youngberg 1964). *Abies amabilis*, *Acer macrophyllum*, *Picea sitchensis*, and *Pinus contorta* also have high nitrogen contents. *Picea sitchensis* seedlings, though higher in nitrogen concentration, have less phosphorus than *Pseudotsuga menziesii* seedlings of similar age when grown in sand culture (van den Driessche 1969).

Larix occidentalis seems to have the highest phosphorus concentration, *Pinus contorta* the lowest (Tarrant et al. 1951, Daubenmire 1953). *Populus tremuloides* heads the list for potassium; *Pinus albicaulis* places last (Dabenmire 1953). *Thuja plicata* foliage apparently has less sulfur than the foliage of *Abies lasiocarpa*, *A. amabilis*, *Pinus contorta*, *Picea engelmannii*, *P. sitchensis*, *Pseudotsuga menziesii*, or *Tsuga heterophylla*; and *T. heterophylla* foliage seems to have slightly less sulfur than that of *P. menziesii* Beaton, Moss et al. 1965).

MICRONUTRIENT CONCENTRATIONS

Micronutrient levels in foliage often are influenced by "luxury consumption," and may reflect soil differences rather than species differences. When Landis (1976) compared foliage nutrient levels in "ideal" seedlings of three Rocky Mountain tree species growing in the same Colorado nursery, however, he found manganese concentrations to be higher in *Picea engelmannii* than in *Pinus contorta* or *P. ponderosa*. Zinc and boron concentrations were higher in *P. contorta* than in *P. ponderosa* or *Picea engelmannii* in these nursery seedlings. Beaton, Brown, et al. (1965), measured micronutrient concentrations in the foliage of three British Columbia conifers. They found that manganese and aluminum levels tended to be higher in *Tsuga heterophylla* needles than in those of *Pseudotsuga menziesii*, which had much more silica than *T. heterophylla*. *P. menziesii* also may have more silica (and less potassium) than *Arbutus menziesii* (Young 1974). Unfortunately, Young's analyses were based on only one tree of each species, and replicated *Pseudotsuga*-*Arbutus* comparisons are not available.

NUTRIENT DEFICIENCY TOLERANCES

Species tolerances of nutrient deficiencies or excesses and differing species growth responses to various nutrient conditions probably are of more immediate concern than species nutrient concentrations. Relative tolerances of nutrient. deficiences are listed in table 9.

Nitrogen deficiencies are best tolerated by *Picea sitchensis*, least tolerated by *Thuja plicata*, *Pinus monticola*, and *P. ponderosa* (Krajina 1970). *Pseudotsuga menziesii* var. *menziesii* also is intolerant of nitrogen deficiencies (Murison 1961). Nitrogen stimulates its shoot growth in relation to root growth but does just the opposite for *Thuja plicata*, decreasing top growth in relation to root growth (Smith et al. 1968).

Table 9--Relative tolerance of macronutrient deficiencies in northwestern tree species[1]

Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	Sulfur
Picea sitchensis	*Pinus ponderosa, P. monticola, Tsuga heterophylla, Thuja plicata*	*Picea engelmannii*	*Tsuga heterophylla*	*Tsuga heterophylla*	*Picea engelmannii*
Tsuga heterophylla	*Pseudotsuga menziesii* var. *menziesii*	*Pseudotsuga menziesii* var. *menziesii*	*Picea sitchensis*	*Pseudotsuga menziesii* var. *menziesii*	*Pseudotsuga menziesii* var. *glauca*
Pseudotsuga menziesii	*Pseudotsuga menziesii* var. *glauca*	*Pinus monticola*	*Pseudotsuga menziesii*	*Pinus monticola*	*Pinus monticola*
Thuja plicata, Pinus monticola, P. ponderosa	*Picea sitchensis*	*Pinus ponderosa*	*Pinus monticola, Thuja plicata, Chamaecyparis nootkatensis, Pinus ponderosa*	*Pseudotsuga menziesii* var. *glauca*	*Pseudotsuga menziesii* var. *menziesii*
		Pseudotsuga menziesii var. *glauca*		*Picea sitchensis*	*Pinus ponderosa*
				Thuja plicata, Chamaecyparis nootkatensis	

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[1] Most of the information used in compiling this table was obtained from Krajina (1959, 1970). Tolerant species are listed above intolerant species. Information is insufficient to separate species grouped together.

Picea sitchensis growth is stimulated more than *Pseudotsuga menziesii* growth by high nitrogen levels (van den Driessche 1968), and *P. sitchensis* should surpass *P. menziesii* on high-nitrogen, coastal sites.

Psuedotsuga menziesii is less tolerant of phosphorus deficiences than *Pinus ponderosa, P. monticola, Tsuga heterophylla,* or *Thuja plicata* (Krajina 1970). It is more tolerant of low phosphorus than *Picea sitchensis* (van den Driessche 1968, Krajina 1970) or *P. engelmannii* (Murison and Krajina, summarized in Krajina 1970).

Pseudotsuga menziesii var. *menziesii* tolerates phosphorus, potassium, and magnesium deficiencies better than *P. menziesii* var. *glauca,* but is less tolerant of low sulfur (Krajina 1970). Krajina and his co-workers have shown *Tsuga heterophylla* to be more tolerant of calcium and magnesium deficiens than *P. menziesii,* while *Thuja plicata* is less tolerant. Using a "replacable calcium gradient" Waring and Major (1964) ranked *Libocedrus decurrens* as more tolerant of calcium deficiencies than either *P. menziesii* or *Arbutus menziesii.*

Although comparative species responses to nutrient deficiencies apparently vary with the deficient nutrient, several authors have compared the general tolerance of two or more northwestern tree species to all nutrient deficiencies.

In general, *Tsuga heterophylla* seems to be more tolerant of soil nutrient deficiencies than *Pseudotsuga menziesii* (Krajina 1970, Heilman and Ekuan 1973), *Abies amabilis* (Krajina 1970), or *A. grandis* (Aldhous and Low 1974). Indeed, *T. heterophylla*'s soil nutrient requirements are among the lowest known for any coniferous tree (Krajina 1970). Although they often grow on ultramafic soils and are not directly compared with *T. heterophylla* in the literature, *Picea breweriana* and *Pinus jeffreyi* may be comparable to it with respect to nutrient deficiencies--they are more tolerant of low fertility than *Abies concolor, A. magnifica* var. *shastensis, Pinus lambertiana, Pseudotsuga menziesii,* or *Tsuga mertensiana* (Waring et al. 1975).

Pseudotsuga menziesii (Gessel et al. 1951) and *Abies amabilis* (Krajina 1970) tolerate poorer nutrient conditions than *Thuja plicata. Pinus lambertiana* is more sensitive than *Pseudotsuga menziesii* to poor supplies of calcium and magnesium (Krajina 1970), but it is better able to utilize infertile ultrabasic soils than *Abies magnifica* var. *shastensis* or *Tsuga mertensiana* (Waring 1970). Infertile soils also are better utilized by *Pinus contorta* than by *Abies lasiocarpa* (Wali and Krajina 1973).

NUTRIENT EXCESSES

Nutrient excesses may be just as limiting as deficiencies, but they occur less frequently. Along the Pacific Coast, *Picea sitchensis* is able to tolerate the excess magnesium in sea spray better than *Tsuga heterophylla* and other conifers (Krajina 1970). Applications of lime are tolerated by *Pseudotsuga menziesii* better than by *T. heterophylla* (Heilman and Ekuan 1973), and *Thuja plicata* is more tolerant of excess calcium than other northwestern trees (Aldhous and Low 1974). *Thuja plicata* also is more tolerant of alkaline soils than *Picea sitchensis, Tsuga heterophylla,* or *Pinus contorta* (Benzian 1965). Acidic soils are tolerated better by *Tsuga heterophylla* than by *Pseudotsuga menziesii* (Heilman and Ekuan 1973).

AMMONIUM VS. NITRATE NITROGEN

In addition to nutrient quantities (deficiencies, optimal amounts, or excesses), nutrient qualities and chemical formulations are important when comparing the survival and growth of tree species. Nitrogen is particularly noteworthy in this respect. Ammonium nitrogen is tolerated by seedlings of *Tsuga heterophylla* (Taylor 1935, Krajina 1970 and 1971, Madoc-Jones 1970, Heilman and Ekuan 1973) and *Pinus contorta* (Madoc-Jones 1970, Krajina 1971). Van den Driessche (1971) found that *Pseudotsuga menziesii* seedlings grew better with ammonium nitrogen than with nitrate nitrogen;

but Krajina et al. (1973) recorded contrary results...their *P. menziesii* and *Pinus contorta* seedlings grew better when supplied with nitrate nitrogen. Mycorrhizal differences may be responsible for these differing results. Without mycorrhizae, nitrates are relatively poor sources of nitrogen for *Pseudotsuga menziesii* seedlings, and growth is better with ammonium nitrate (Li et al. 1972). *Alnus rubra* grows better than *P. menziesii* without mycorrhizae or ammonium, for *A. rubra* roots are capable of reducing nitrate. *P. menziesii* roots are not (Li et al. 1972).

A mixture of both ammonium and nitrate nitrogen appears to be best for *Picea engelmannii* (Krajina 1970), *P. sitchensis* (van den Driessche 1971), *Thuja plicata* and *Tsuga heterophylla* (Krajina et al. 1973). *Abies amabilis*, *A. grandis*, and *Chamaecyparis nootkatensis* seem to prefer nitrate nitrogen.

MYCORRHIZAL RELATIONSHIPS

A review of autecological characteristics would be incomplete without further mention of mycorrhizae, for most woody plants depend upon mycorrhizal fungi for absorption of nutrients from the soil (Trappe 1977). Many species of mycorrhizal fungi are involved. Only three mycorrhizal types occur on northwestern trees, however--the vesicular-arbuscular mycorrhizae, the ectomycorrhizae + ectendomycorrhizae, and the ericoid mycorrhizae.[3] Individual trees usually have several species of mycorrhizal fungi on their roots (Trappe 1977), but these species tend to be all of the same mycorrhizal type...and different tree species support different types (table 10).

Trappe (1977) demonstrated with *Pinus ponderosa*, *Tsuga heterophylla* and *Pseudotsuga menziesii* that different host species can react differently to a given mycorrhizal fungus. In Trappe's experiment, inoculation with pure cultures of four mycorrhizal fungi increased *T. heterophylla* seedling weights, but not the weights of *P. ponderosa* or *Pseudotsuga* seedlings. Similar data on the mycorrhizal responses of other northwestern tree species have been published, but they are too scanty and variable as yet to provide much useful information. The autecological characteristics of mycorrhizal fungi need further study before they can be related to the autecological characteristics of northwestern tree species in more detail.

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[3] James M. Trappe, Forestry Sciences Laboratory, Corvallis, Oreg. Personal communication, June 1978.

Table 10--Types of mycorrhizae associated with northwestern tree species[1]

Vesicular-arbuscular mycorrhizae	Ectomycorrhizae + ectendomycorrhizae	Ericoid mycorrhizae
Acer macrophyllum	*Abies amabilis*	*Arbutus menziesii*
Acer negundo	*Abies concolor*	
Chamaecyparis lawsoniana	*Abies grandis*	
Chamaecyparis nootkatensis	*Abies lasiocarpa*	
Fraxinus oregona	*Abies magnifica*	
Juniperus occidentalis	*Abies magnifica* var. *shastensis*	
Juniperus scopulorum	*Abies procera*	
Libocedrus decurrens	*Alnus rubra*	
Populus balsamifera	*Betula papyrifera*	
Populus tremuloides	*Castanopsus chrysophylla*	
Populus trichocarpa	*Larix laricina*	
Sequoia sempervirens	*Larix lyalli*	
Taxus brevifolia	*Larix occidentalis*	
Thuja plicata	*Lithocarpus densiflora*	
Umbellularia californica	*Picea breweriana*	
	Picea engelmannii	
	Picea glauca	
	Picea mariana	
	Picea sitchensis	
	Pinus albicaulis	
	Pinus attentuata	
	Pinus contorta	
	Pinus jeffreyi	
	Pinus lambertiana	
	Pinus monticola	
	Pinus ponderosa	
	Populus balsamifera	
	Populus tremuloides	
	Populus trichocarpa	
	Pseudotsuga menziesii	
	Quercus chrysolepis	
	Quercus garryana	
	Quercus kelloggii	
	Tsuga heterophylla	
	Tsuga mertensiana	

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[1] James M. Trappe, Forestry Sciences Laboratory, Corvallis, Oreg. Personal communication, June 1978.

GROWTH

Light, temperature, moisture, nutrients, and other environmental factors all influence growth rates; and species growth rates should not be treated as separate entities. Growth is the result of genetic-environmental interactions that vary with both species and environment. One can compare species under given environmental conditions and derive rankings based upon species growth in those conditions. For example, Godman (1949) found that *Picea sitchensis* diameter growth outstripped that of *Tsuga heterophylla* in coastal Alaska, and Johnstone (1976) measured faster juvenile height growth of *Pinus contorta* than of *Picea glauca* in west-central Alberta. Unfortunately, such local comparisons reflect differential species reactions to particular light, temperature, moisture, and/or nutrient conditions. They may not reflect species growth rates as such, for different species often grow differently in different environments.

Several examples illustrate the interactions between growth rate and environment. Walters, Soos, and Ker (1961) observed that *Thuja plicata* seedlings reached breast height faster than *Pseudotsuga menziesii* seedlings on good sites in British Columbia. On poor sites the species ranking was reversed, with *P. menziesii* seedlings growing fastest and *T. plicata* seedlings slowest. Walters and Haddock (1966) concluded that inherent species vigor is better expressed on high quality sites than on poor sites, and they rated *Tsuga heterophylla* as faster growing than *Thuja plicata* or *Abies amabilis*. Nevertheless, growth-site interactions are confusing.

Stein (1963) planted *Pinus ponderosa, P. lambertiana, Libocedrus decurrens, Pseudotsuga menziesii,* and *Abies grandis* seeds from the same seed sources on three kinds of soil in southwestern Oregon. The resulting seedling height growth comparisons differed with soil type...*Libocedrus decurrens* ranked first on one soil, fourth on another

Pinus monticola site index and tree heights of several associated species in northern Idaho, they found that species height rankings varied with both site index and stand age. *Pseudotsuga menziesii* was taller than *Pinus monticola, Tsuga heterophylla,* or *Abies grandis* in 30-year-old stands of site index 40, shorter than these three species in 30-year-old stands of site index 80.

Clearly, ranking growth rates as such is impractical. Nevertheless, species do grow differently. Roots develop more rapidly in some than in others, seasonal shoot growth periods vary in length, mature sizes differ, and the species have different life spans. As recorded in the literature, these differences are summarized in table 11.

SEEDLING ROOT GROWTH RATE

Pinus ponderosa seedlings characteristically develop deep, sturdy root systems more rapidly than their associates (Pearson 1924, Stein 1955 and 1963, Tarrant 1953). *P. lambertiana* seedlings also develop root systems very rapidly. *Libocedrus decurrens* (Stein 1963) and *Pinus contorta* (Tarrant 1953) root development is somewhat slower.

Pseudotsuga menziesii, Abies grandis, Pinus monticola, and *Larix occidentalis* may be ranked next (see Haig et al. 1941, Stein 1955 and 1963). Seedling root growth rates in these species are faster than those of *Thuja plicata* and *Tsuga heterophylla* (Haig et al. 1941). As *Tsuga heterophylla* root penetration is poorer than that of *Thuja plicata* (Boyd 1959), it probably is also slower. *Tsuga heterophylla* probably is not the slowest species, however, for Ruth (1968a) found *Picea sitchensis* roots to be even shorter than those of *Tsuga heterophylla* after the first growing season.

Picea engelmannii seedlings produce roots more slowly than *Pseudotsuga menziesii* (Pearson 1924) or *Abies lasiocarpa* (Smith 1955) seedlings, and *Abies grandis*

Table 11--Relative root growth rates, shoot growth periods, mature sizes, and longevity of northwestern tree species[1]

Seedling root growth rate[2]	Shoot growth period[3]	Size at maturity[4]		Longevity[4]
		Diameter	Height	
Pinus ponderosa, P. lambertiana	*Thuja plicata, Libocedrus decurrens*	*Sequoia sempervirens*	*Sequoia sempervirens*	*Sequoia sempervirems, Thuja plicata, Chamaecyparis nootkatensis*
Libocedrus decurrens, Pinus contorta	*Pinus ponderosa, P. jeffreyi, Chamaecyparis lawsoniana*	*Thuja plicata*	*Pseudotsuga menziesii*	*Picea sitchensis*
Pseudotsuga menziesii, Pinus monticola, Larix occidentalis	*Tsuga heterophylla*	*Picea sitchensis*	*Picea sitchensis*	*Pseudotsuga menziesii*
Thuja plicata	*Picea sitchensis, P. glauca*	*Pseudotsuga menziesii*	*Abies procera*	*Larix occidentalis*
Tsuga heterophylla	*Sequoia sempervirens*	*Chamaecyparis lawsoniana*	*Tsuga heterophylla*	*Pinus ponderosa*
Picea sitchensis	*Pinus contorta*	*Larix occidentalis*	*Thuja plicata*	*Chamaecyparis lawsoniana, Libocedrus decurrens, Picea engelmannii, Quercus garryana*
	Abies grandis	*Abies concolor, A. procera, Chamaecyparis nootkatensis*	*Chamaecyparis lawsoniana, Pinus monticola*	*Abies amabilis, A. procera, Pinus lambertiana, P. monticola, Tsuga heterophylla, T. mertensiana*
	Pseudotsuga menziesii	*Abies magnifica, Pinus lambertiana*	*Abies grandis*	*Abies concolor, A. grandis, A. magnifica, Acer macrophyllum*
	Abies procera	*Libocedrus decurrens, Tsuga heterophylla*	*Abies amabilis, Pinus lambertiana*	*Abies lasiocarpa, Pinus contorta*
	Abies amabilis	*Pinus monticola*	*Larix occidentalis*	*Populus trichocarpa*
	Abies concolor, Pinus lambertiana	*Abies grandis, Pinus ponderosa*	*Picea engelmannii*	*Lithocarpus densiflora*
		Abies amabilis	*Abies concolor*	*Alnus rubra*
		Picea engelmannii	*Abies magnifica*	
		Tsuga mertensiana	*Libocedrus decurrens*	
		Populus trichocarpa	*Pinus ponderosa*	
		Lithocarpus densiflora	*Chamaecyparis nootkatensis, Alnus rubra*	
		Quercus garryana	*Abies lasiocarpa, Pinus contorta, Tsuga mertensiana, Populus trichocarpa*	
		Alnus rubra	*Lithocarpus densiflora*	
		Abies lasiocarpa	*Quercus garryana*	
		Pinus contorta, Acer macrophyllum		

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[1] Fast growing, large or long-lived species are at the tops of these columns; slow growing, small or short-lived species are at the bottoms. Species with long growth periods are ranked above those with short periods. Information is insufficient to separate species grouped together.

[2] From Pearson (1924), Haig et al. (1941), Stein (1955, 1963), Tarrant (1953), Boyd (1959), and Ruth (1968a). Rankings were based upon total root length comparisons of equal-age seedlings. Seedling ages varied from 3 months to 2 years.

[3] From Fowells (1941), Buckland (1956), Walters and Soos (1963), Mitchell (1965), and Williams (1968).

[4] From Franklin, Jerry F., and C. T. Dyrness (1973).

these species have not been compared enough with others to permit ranking in table 11.

SHOOT GROWTH PERIOD

In a given locality, some species begin shoot growth earlier in the spring than others. For example, *Pseudotsuga menziesii* breaks bud before *Quercus garryana* in the Willamette Valley of western Oregon (Thilenius 1964), and low-elevation *P. menziesii* trees begin growing several days ahead of associated *Abies grandis* trees in northeastern Oregon (Wickman 1976). Shoot growth initiation dates are extremely variable, however, both within and among species.

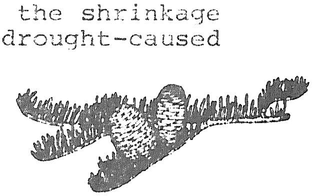
Relative growing season lengths apparently are more constant when species are compared...long-season species tend to have longer growing periods than short-season ones whenever they are grown together. Fowells (1941) measured the height growth periods of six northwestern species for 8 years in the Sierra Nevada of California. *Libocedrus decurrens* had the longest growing season, followed by *Pinus ponderosa* and *P. jeffreyi*, *P. contorta*, *Abies concolor*, and *Pinus lambertiana*.

Thuja plicata shoots grow for a longer period than those of *Pinus contorta*, and *P. contorta* has a longer growing season than *Tsuga heterophylla* in the Cascade Mountains of Oregon (Williams 1968). Williams observed that *Tsuga heterophylla*'s growing season exceeded those of *Abies lasiocarpa*, *A. procera*, *A. amabilis*, *Tsuga mertensiana*, and *Pseudotsuga menziesii*. Similar observations were made by Walters and Soos (1963) in southwestern British Columbia. Like Williams, they found that *Thuja plicata* had the longest growing season. *Tsuga heterophylla* had a longer season than *Pseudotsuga menziesii*, which grew for a longer period than *Pinus monticola*. Buckland (1956), also working in southwestern British Columbia, noted that *Pseudotsuga menziesii* and *Abies grandis* ceased shoot growth earlier and more abruptly than *Tsuga heterophylla* and *Thuja plicata*.

Perhaps the most extensive study of shoot growth periods was accomplished by Mitchell (1965), in England. He compared 25 conifer species for four to six seasons. *Thuja plicata* led the northwestern species for a mean length of growing season, followed in order by *Chamaecyparis lawsoniana*, *Tsuga heterophylla*, *Picea sitchensis*, *P. glauca*, *Sequoia sempervirens*, *Pinus contorta*, *Abies grandis*, *Pseudotsuga menziesii*, *Abies procera*, *A. amabilis* and *A. concolor*.

RADIAL GROWTH PERIOD

Godman and Gregory (1953) found that the radial growth of *Picea sitchensis* near Juneau, Alaska occurred over a longer period than that of *Tsuga heterophylla*. This longer radial growth period may contribute to the greater size of *P. sitchensis*, but similar growth period-tree size relationships are not consistently evident among other species. Although the radial growth period of *Alnus rubra* is shorter than the growth periods of the larger *Pseudotsuga menziesii* and *Thuja plicata* (Reukema 1965), the radial growth period of *Abies concolor* is significantly shorter than growth periods of the smaller *Pinus ponderosa* and *Libocedrus decurrens* (Fowells 1941)...and *Sequoia sempervirens* begins growth later than *Abies concolor* in northern California (Bawcom et al. 1961). Growth rate probably is more important than length of growth period in determining mature tree sizes. Sometimes these growth rates are somewhat erratic. While comparing the radial growth of *Abies grandis*, *Larix occidentalis*, *Pinus ponderosa*, and *Thuja plicata* in northern Idaho, Daubenmire (1946) recorded a second September growth spurt. This second spurt occurred only in *Thuja plicata* at low elevations, however, and Daubenmire's radial growth observations may have been affected by the shrinkage associated with drought-caused dehydration.



REPRODUCTION

VEGETATIVE REPRODUCTION

Unlike all other northwestern conifers, *Sequoia sempervirens* reproduces vegetatively by producing vigorous stump sprouts (Harlow and Harrar 1950). *Picea sitchensis*, *Tsuga heterophylla*, and *T. mertensiana* occasionally reproduce by branch-layering (Cooper 1931). *Thuja plicata*, *Chamaecyparis nootkatensis*, *Picea mariana*, *Larix laricina*, and *Abies lasiocarpa* also reproduce vegetatively by developing adventitious roots on low-hanging limbs, broken-off branches, and fallen live boles (Hustich 1953, Schmidt 1955). This vegetative regeneration is as important as reproduction from seed in high density *Thuja plicata* forests (Schmidt 1955), but it seldom occurs in *Abies lasiocarpa* (Cooper 1911). Although northwestern hardwood species (*Alnus rubra*, *Acer* spp., *Quercus* spp. etc.) also develop adventitious roots and stump sprouts, reproduction of northwestern tree species usually involves the production, dissemination, and germination of seeds.

SEED PRODUCTION

Seed production begins at younger ages in some species than in others. The species ranking in table 12 illustrates this in a general way. More detailed comparisons are available for several of these species, but they are difficult to include in an overall comparison. For example, *Abies lasiocarpa* begins to bear seed earlier in life than *Picea engelmannii* (Le Barron and Jemison 1953), but additional information that would relate these species to others in table 12 is lacking.

Additional reproductive differences become evident when seed producing trees of different species are compared. Some develop strobili earlier than others in the spring, and seed dissemination does not occur simultaneously in the fall (table 12). Studying the effects of elevation and climatic factors on production and dispersal of

Island, Ebell and Schmidt (1959) found that anthesis occurred first in *Thuja plicata* and *Chamaecyparis nootkatensis*, last in *Tsuga mertensiana*. *Pseudotsuga menziesii* and *T. heterophylla* produced pollen earlier than the *Abies* species on Vancouver Island. Pollen production for *Abies amabilis*, *A. grandis*, and *A. lasiocarpa* occurs somewhat earlier than for *A. procera* in the Cascades (Franklin and Ritchie 1970).

SEED DISSEMINATION

Seed dissemination occurs during a period of several months for most species. Nevertheless, northwestern species differ rather conspicuously when intial seed dissemination dates, rates, and peak periods are compared. *Picea sitchensis* seeds mature earlier than *Tsuga heterophylla* seeds in southeastern Alaska (Harris 1969).

In the somewhat similar environments of western British Columbia, *Abies grandis* and *A. amabilis* seedfalls begin before the seedfall of *Thuja plicata* (British Columbia Forest Service 1950, Garman 1951, 1955, and Hetherington 1965). Then *Thuja plicata*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* begin to drop their seeds, with *P. menziesii* slightly ahead of *T. plicata*, and *T. heterophylla* beginning last (British Columbia Forest Service 1950). *Abies grandis* seed dispersal is completed first, followed by almost all of the *Thuja plicata* seeds, then *P. menziesii*, and finally *T. heterophylla* (British Columbia Forest Service 1950, Garman 1951, 1955). A few *Thuja plicata* seeds must remain in the cones for many months, however, for Pickford (1929) observed *T. plicata* seedfall in July and August of the year following initial seed dissemination.

Farther south, *Abies amabilis* seedfall precedes that of *A. procera* in the Cascade Range (Franklin and Ritchie 1970). *Pinus monticola* seed dissemination occurs before that of *Abies grandis* in the western white pine type, and *A. grandis* seedfall is followed by *Larix occidentalis* and *P. menziesii*. The last species to disseminate seed in the western white pine type are

Table 12--Comparisons of minimum seed bearing ages, anthesis order, and initial seed dissemination times of northwestern tree species[1]

Minimum seed bearing ages[2]	Anthesis[3]	Initial seed dissemination[4]
Arbutus menziesii	*Thuja plicata, Chamaecyparis nootkatensis*	*Populus tremuloides, Populus trichocarpa*
Pinus contorta	*Pseudotsuga menziesii*	*Pinus monticola, P. lambertiana, P. ponderosa*
Pinus jeffreyi, Alnus rubra, Pseudotsuga menziesii var. *menziesii, Sequoia sempervirens, Acer macrophyllum, Populus trichocarpa*	*Tsuga heterophylla*	*Abies grandis, A. amabilis*
Abies procera, Pinus ponderosa, Pinus monticola, Chamaecyparis lawsoniana, Populus tremuloides	*Abies grandis*	*Pseudotsuga menziesii, Abies concolor, Larix occidentalis, Libocedrus decurrens, Pinus contorta, P. jeffreyi, Picea engelmannii, Chamaecyparis lawsoniana*
Thuja plicata, Picea sitchensis, Abies grandis, Pseudotsuga menziesii var.*glauca*	*Abies amabilis*	*Abies magnifica* var. *shastensis, Thuja plicata*
Tsuga heterophylla, T. mertensiana, Larix occidentalis, Pinus albicaulis	*Pinus contorta*	*Abies lasiocarpa, A. procera, Picea sitchensis*
Larix lyalli, Abies amabilis	*Pinus monticola*	*Chamaecyparis nootkatensis, Tsuga heterophylla*
Quercus kelloggii, Picea glauca	*Abies lasiocarpa*	
Abies magnifica, A. magnifica var. *shastensis, A. concolor*	*Abies procera, Tsuga mertensiana*	
Pinus lambertiana		

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[1] The species are ranked from youngest and earliest (top) to oldest and latest (bottom). Where species are absent or occur in the same group, information is insufficient to include or separate them.

[2] Compiled from information obtained from For. Serv. Agric. Handb. No. 450 (1974).

[3] Compiled from the data of Ebell and Schmidt (1959) and Franklin and Ritchie (1970).

[4] Compiled from information published by Pickford (1929), Haig et al. (1941), British Columbia For. Serv. (1950), Garman (1951, 1955), Hetherington (1965), Gashwiler (1969), Harris (1969), Franklin and Ritchie (1970), For. Serv. Agric. Handb. No. 450 (1974), and Wang (1974).

(Haig et al. 1941). *Thuja plicata* and *Tsuga heterophylla* seedfall also occur later than that of *P. menziesii* in west-central Oregon (Gashwiler 1969).

Early *Abies amabilis* seed dissemination may be the results of active cone disintegration--scales literally tear themselves off the cone axis as they distort in drying. *A. grandis* and *A. lasiocarpa* cones also disintegrate, but less actively; *A. procera* cones remain intact until wind action or branch movement disturbs them (Franklin and Ritchie 1970). No obvious cone structure or modification seems to be responsible; but *Tsuga heterophylla* releases seed more slowly than most northwestern trees, regardless of location (Haig et al. 1941, British Columbia Forest Service 1950, Garman 1951 and 1955, Hetherington 1965, Gashwiler 1969, and Harris 1969).

SEED CROP SIZE

Quantity of seeds produced in a seed crop probably is more important than when those seeds are disseminated. Unfortunately, seed crop sizes vary with seasons as well as with species. As a result, observers comparing species in different years often rank species differently. Seed production also varies with locations and with tree age to further complicate species comparisons. For example, Gregory (1957, 1958, 1959) and Harris (1960, 1962) recorded larger average cone crops for *Picea sitchensis* than for *Tsuga heterophylla* during most years in Alaska. In contrast, Ruth and Berntsen (1955) found that *T. heterophylla* "...was a more prolific seed producer..." than *P. sitchensis* in coastal Oregon. Similar observer differences occur with other species. They were reconciled whenever possible in constructing table 13. Where reconciliation was unnecessary (e.g.,

Table 13--Comparative seed crop sizes and frequencies of northwestern tree species[1]

Seed crop size[2]	Seed crop frequency[3]
Thuja plicata, Tsuga heterophylla, Chamaecyparis nootkatensis, C. lawsoniana, Picea sitchensis, Larix occidentalis	*Acer macrophyllum, A. negundo, Populus trichocarpa*
Pseudotsuga menziesii, Pinus contorta, P. jeffreyi	*Pinus monticola, P. contorta*
Pinus ponderosa	*Tsuga mertensiana, T. heterophylla, Abies lasiocarpa, A. grandis, A. amabilis, Picea engelmannii, Thuja plicata*
Pinus lambertiana	*Pseudotsuga menziesii, Larix occidentalis*
Abies concolor	*Pinus ponderosa, Picea mariana, Populus tremuloides*
Abies magnifica	

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[1] Species with the largest or most frequent seed crops are at the top, those with smallest or least frequent crops are at the bottom. Where species are omitted or occur in the same group, information is insufficient to include or separate them.

[2] Compiled from information published by Boe (1953), Garman (1955), Fowells and Schubert (1956), Gashwiler (1969), Gordon (1970), and Zobel (see footnote 2, page 5).

[3] Compiled from information published by Boe (1954), Franklin (1968), Franklin et al. (1974), Wang (1974), and Dahms and Barrett (1975).

Garman 1955, Gashwiler 1969), species were ranked without further comment. Where reconciliation was impractical or where sufficient information was lacking, species were discussed, but not included in table 13.

Sequoia sempervirens is a prolific seed producer. Its seed crops are larger than those of *Pinus ponderosa* (Schubert and Adams 1971). Comparing trees of similar size in northern California, Fowells and Schubert (1956) found that *Pinus ponderosa* produced more cones than *P. lambertiana*. When large trees were compared, both *Pinus* species had more cones than *Abies concolor*. Nevertheless, *Abies concolor* produces more sound seeds than *A. magnifica* (Gordon 1970). Schubert and Adams (1971) ranked *Libocedrus decurrens* last in seed production, below *A. magnifica*.

Comparisons with other species are lacking, but Dobbs (1972) found seed production in *Picea glauca* stands to be much higher than production in *P. engelmannii* stands in interior British Columbia. Southward, in northwestern Montana, Boe (1953) counted many more *Larix occidentalis* seeds than *Pseudotsuga menziesii* seeds at the edge of a mixed *Larix-Pseudotsuga* stand. Unfortunately, such stand comparisons are affected by the number of trees in each species that make up the stand. Zobel[4] calculated numbers of seeds per square meter of basal area for each species in his sample stands. Measuring seed crops for 2 seed years, he found *Tsuga heterophylla* to be a better seed producer than *Chamaecyparis lawsoniana*, which produced more seeds than either *Abies concolor* or *Pseudotsuga menziesii* when compared on a basal area basis. When Franklin et al. (1974) compared upper slope species with respect to the number of seeds produced per tree over a 12-year period, they ranked them as follows:

Abies procera (most seeds)
Picea engelmanni
Tsuga mertensiana
Abies grandis, *A. concolor*
Abies amabilis
Abies magnifica var. *shastensis*
Pinus monticola (fewest seeds).

SEED CROP FREQUENCY

Although seasonal and location variation probably account for most of the differences in relative seed quantitites recorded by different observers for the same species, variation in seed crop frequency (table 13) also must have affected their data and conclusions. Some species, *Pinus monticola* (Franklin 1968, Franklin et al. 1974) for example, produce seeds quite regularly. Others, like *Thuja plicata* (Gashwiler 1969), are erratic and produce a large crop one year and no crop at all for the next year or two.

Although most species seem to be rather intermediate with respect to seed crop frequency, *Tsuga heterophylla* tends to be more frequent than *Picea sitchensis* (Meyer 1937). In Montana, *Pinus contorta* seed crops are more frequent than *Larix occidentalis* crops, which are more frequent than those of *P. ponderosa* (Boe 1954). *Pinus contorta* seed crops also are more frequent than *P. ponderosa* crops in Oregon (Dahms and Barrett 1975). In interior British Columbia, where *Picea engelmannii* and *P. glauca* hybridize, good *P. engelmannii* seed crops are more frequent than good *P. glauca* crops (Dobbs 1972). Wang (1974) published a general summary of seed crop frequencies for 21 northwestern tree species.

SEED SOUNDNESS

Efficacy of any seed crop, regardless of its frequency, is dependent upon sound seeds in that crop. Few species comparisons are available; but *Pinus lambertiana*, *P. ponderosa*, and *Libocedrus decurrens* seed crops have higher proportions of sound seed than *Abies*

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[4] Zobel, Donald B. Seed production in forests of *Chamaecyparis lawsoniana*.

Schubert 1956). Gashwiler (1969) found more filled seed in *Thuja plicata* than in *Tsuga heterophylla* or *Pseudotsuga menziesii* during the 12 years he monitored seed fall in west-central Oregon.

SEED FLIGHT

Several important characteristics of seed fall (speed and dispersal distance, for example) are functions of seed weight and structure. Average seed weights of northwestern species are listed in table 14. Seed structures vary greatly. Rather than comparing them as such, several investigators have measured seed flight to compare species seed distribution directly.

Siggins (1933) seems to have done the definitive work in seed flight measurements. After dropping seeds of 13 western conifers down an elevator shaft in the campanile, University of California, Berkeley, he concluded that *Tsuga heterophylla* seeds fell the slowest, *Pinus lambertiana* seeds the fastest. In a less-precise experiment, Isaac (1930) released seeds from a box kite and a pilot balloon under varying wind conditions. He measured the flights of *Tsuga heterophylla, Pinus monticola, Pseudotsuga menziesii, Abies procera, Thuja plicata,* and *Pinus ponderosa* seeds over snow covered fields and found them to be in the order given--*Tsuga heterophylla* seeds flying farthest, *Thuja plicata* and *Pinus ponderosa* seeds landing closest to the release point. Pickford (1929) and Gashwiler (1969) also concluded that *Tsuga heterophylla* seeds fly farther than *Thuja plicata* seeds.

In British Columbia and southeastern Alaska, *Tsuga heterophylla* seed flights may be shorter than the flights of *Thuja plicata* (Garman 1951) or *Picea sitchensis* (Godman 1953b) seeds. These northern conclusions were based upon indirect observations rather than direct measurements, however, and unequal consumption by animals or different tree heights and densities may have influenced the

Using seed trap transects extending outward from clearcut edge Carkin et al. (1978) found that *Abies procera* seed fall declined more rapidly than that of *A. amabilis* in the Washington and Oregon Cascade Range. *Picea engelmannii* seeds fly further than *P. glauca* seeds (Dobbs 1972). Oth comparisons are summarized in table 14.

SEED DURABILITY AND LONGEVITY

Both long and short seed flight separate seeds from their parent cones and expose them to environmental stresses that must be endur until germination is accomplished. *Pinus monticola* (Hofmann 1925), *P. contorta,* and *P. ponderosa* (Wright 1931) seeds are more resistant to high temperatures than *Pseudotsuga menziesii* seeds. When seeds are stored for long periods under cool temperature conditions, the *Pinus* species again seem to be more resistant and long-lived (Isaac 1940 and 1943, Schubert 1954, Holmes and Buszewicz 1958). Other species longevity comparisons are summarized in table 15.

SEED GERMINATION

Given similar environmental conditions, *Pseudotsuga menziesii* seeds usually are easier to germinate than *Pinus monticola* or *P. lambertiana* seeds (Allen and Bientjes 1954). Similar differences have been noted by other workers, using other species. For example, Dobbs (1972) found *Picea engelmannii* seeds to have "...on the average, higher germinative energy and higher germinative capacity..." than *P. glauca* seeds. Germination rates and stratification requirements are compared in table 16.

Species germination rates have been compared more than other germination attributes. *Abies procera* seeds germinated faster than *A. magnifica* var. *shastensis* seeds when covered with 1/2 inch (1.3 cm) of mineral soil, and

Table 14--Comparative seed weights and seed flight distances of northwestern tree species

Seed weights[1]	Seed flight distances[2]
Populus tremuloides	*Tsuga heterophylla*
Alnus rubra	*Pinus contorta*
Thuja plicata	*Picea sitchensis*
Tsuga heterophylla	*Pseudotsuga menziesii*
Arbutus menziesii	*Abies amabilis*
Picea glauca	*Pinus ponderosa*
Picea sitchensis, Chamaecyparis lawsoniana	*Thuja plicata*
Larix lyalli	*Abies grandis, A. concolor*
Larix occidentalis	*Libocedrus decurrens*
Picea engelmannii	*Pinus jeffreyi*
Sequoia sempervirens	*Sequoia sempervirens*
Tsuga mertensiana	*Pinus lambertiana*
Chamaecyparis nootkatensis	
Pinus contorta	
Picea breweriana	
Pseudotsuga menziesii	
Abies lasiocarpa	
Pinus monticola	
Abies grandis	
Libocedrus decurrens	
Taxus brevifolia	
Abies procera	
Pinus ponderosa	
Abies concolor, A. amabilis	
Abies magnifica var. *shastensis*	
Abies magnifica	
Pinus jeffreyi, Acer macrophyllum	
Pinus albicaulis, P. lambertiana	
Lithocarpus densiflora, Quercus garryana, Q. kelloggi	

[1] Derived from data published in For. Serv. Agric. Handb. No. 450 (1974). Species with light seeds are listed above those with heavy seeds. Species on the same line have equal seed weights.

[2] Based upon the seedfall measurements of Siggins (1933). Species with long seed flights are listed above those with short flights. Species on the same line have the same flight characteristics. Where species are omitted, data are insufficient for comparison.

monticola seeds in the Cascade Range (Franklin and Hoffman 1968). Further differences are present among both *Abies* and *Pinus* species. Davidson (1959) found *Abies grandis* germination to be faster than that of *A. amabilis*, and Lanquist (1946) observed faster germination in *A. concolor* than in *A. magnifica*. Lanquist's data also showed that *Pinus jeffreyi* seeds germinated which were far ahead of *P. lambertiana* seeds. His data show *Abies concolor* to germinate slightly faster than *Libocedrus decurrens*--a finding that conflicts with an earlier statement by Show (1930) attributing greater rapidity to the *L. decurrens* germination. As Lanquist sowed the *Abies* and *Libocedrus* seeds at different depths, Show's statment probably

Table 15--Comparative seed longevity of northwestern tree species[1/]

Pinus ponderosa
Pinus contorta
Pinus jeffreyi
Pinus lambertiana
Pinus monticola
Pseudotsuga menziesii, Thuja plicata, Chamaecyparis lawsoniana, Tsuga heterophylla, Picea sitchensis
Larix occidentalis
Pinus albicaulis
Abies procera, Tsuga mertensiana, Picea engelmannii
Abies concolor, A. grandis, A. lasiocarpa, A. magnifica, Libocedrus decurrens, Sequoia sempervirens

[1/] Compiled from data published by Schubert (1954) and Holmes and Buszewicz (1958). Species with more longevity are listed above those with less. Information is insufficient to separate species listed in the same group.

Table 16--Comparative germination attributes of northwestern tree species[1/]

Germination rate[2/]	Stratification required[3/]
Pinus jeffreyi, P. ponderosa, Abies procera	*Picea sitchensis, P. engelmannii, P. glauca, Thuja plicata, Chamaecyparis lawsoniana, Tsuga heterophylla, Pinus ponderosa, P. jeffreyi*
Pseudotsuga menziesii, Abies grandis, A. concolor, A. magnifica var. *shastensis, Libocedrus decurrens*	*Abies magnifica* var. *shastensis, A. grandis, A. concolor, A. procera, A. lasiocarpa, A. amabilis, Pseudotsoga menziesii, Pinus contorta*
Pinus lambertiana, P. monticola, Picea engelmannii	*Pinus lambertiana, P. monticola, Acer* species, *Taxus brevifolia*

[1/] Species germinating faster and those requiring less stratification are listed above slower, stratification-dependent species. Where species occur in the same group, information is insufficient for further separation.

[2/] From Lanquist (1946), Murison (1959), Stein (1963), and Franklin and Hoffman (1968).

[3/] From Heit (1968), Kotar (1972), and For. Serv. Agric. Handb. No. 450 (1974).

germination is slower than that of *Pinus ponderosa* (Lanquist 1946, Murison 1959), faster than that of *Tsuga heterophylla* (Gashwiler 1969) or *Pinus lambertiana* (Lanquist 1946, Murison 1959, Stein 1963). Murison (1959) found *Pinus ponderosa* seed germination to be faster than *Pseudotsuga menziesii* var. *glauca*, which was faster than *P. menziesii* var. *menziesii*. Both *Pseudotsuga* varieties germinated faster than *Pinus lambertiana* after a 6-week stratification period. The earliest germination of Murison's stratified *Picea engelmannii* seeds occurred slightly later than that of his stratified *Pinus monticola*.

SEED STRATIFICATION REQUIREMENTS

Seed stratification is essential for the prompt germination of some northwestern tree species, unnecessary for others. Stratification requirements appear to be highest for *Pinus lambertiana*, *P. monticola*, *Taxus brevifolia*, and *Acer* species. *Abies grandis*, *A. procera*, *Pseudotsuga menziesii*, *Picea breweriana*, and stored *Pinus ponderosa* seeds also benefit from a moist, cool pregermination treatment; but *Thuja plicata*, *Picea engelmannii*, *P. sitchensis*, and fresh *Pinus ponderosa* seeds do not require prechilling (Heit 1968, Forest Service, USDA 1974). Although *Abies amabilis* germination occurs faster after stratification for 8 weeks at 4°C, *Tsuga heterophylla* germination is retarded by this treatment (Kotar 1972).

GERMINATION ENVIRONMENTS

Soil attributes have been related to the germination of several northwestern tree species. *Thuja plicata* germination is best in alkaline soil; but *Tsuga heterophylla* germination is depressed there, reaching is optimum under acid conditions (Thrupp 1939). Thrupp, working under poorly controlled greenhouse conditions, concluded that magnesium retards *Picea sitchensis* and *Thuja plicata* germination but accelerates the germination of *Pseudotsuga menziesii* and *Tsuga heterophylla*. The germination of *P. menziesii* is not as sensitive to soil moisture stress as that of *Picea engelmannii* (Brayshaw 1970). Soil moisture may have influenced the results published by Garman (1955). He noted that maximum germination of *Tsuga heterophylla*, *Picea sitchensis*, and *Thuja plicata* occurred in 75-

Pseudotsuga menziesii germination occurred in only 25-percent shade. Moisture's importance certainly was demonstrated by Ackerman (1957), who sowed *Picea glauca* and *Pinus contorta* seeds on both trenched and untrenched seedbeds in Alberta. Where the trenching removed root competition of the residual stand, *P. contorta* germination and survival were benefited but *P. glauca* was not affected.

SEEDBEDS

Seed germination and subsequent seedling survival are greatly affected by seedbed conditions. Although good seedbeds (e.g., mineral soil) tend to be favorable for all northwestern tree species, some species apparently are able to utilize good seedbeds more efficientl than others. Conversely, some species are able to tolerate poor seedbeds better than others. These general seedbed-species relationships are shown for several northwestern trees in table 17.

Lack of available moisture probably contributes to the poor seedbed characteristics of moss, litter, and duff. Surface moss dries out rapidly. *Tsuga heterophylla* seeds apparently germinate better than *Thuja plicata* or *Picea sitchensis* seeds in this moss (Godman 1953a, Phelps 1973)...and the *T. plicata* survival is better than that of either *Tsuga* or *Picea* in southeastern Alaska (Godman 1953a

Moisture associated with shaded conditions probably influenced the germination and survival of Sierra Nevada conifers on the seedbeds subjectively compared by Stark (1965). Stark concluded that *Libocedrus decurrens* germinated best on bare soil in half shade, but *Pinus lambertiana* germination was best on light litter in full sunlight. Survival of both species was judged to be highest where litter occurred.

In greenhouse and laboratory studies, seedbed differences persist even when moisture differences are minimized. An ash seedbed stimulate *Pseudotsuga menziesii* germination but reduced the germination of

Table 17--Comparative seedbed suitability of northwestern tree species[1]

Organic seedbeds		Mineral soil seedbeds		Burned seedbeds
Coastal	Interior	Coastal	Interior	
Tsuga heterophylla	*Picea glauca, Pseudotsuga menziesii*	*Alnus rubra*	*Larix occidentalis, Picea engelmannii*	*Pseudotsuga menziesii, Abies grandis, Pinus ponderosa*
Thuja plicata	*Abies lasiocarpa, Pinus contorta*	*Picea sitchensis*	*Pinus contorta, Abies lasiocarpa*	*Tsuga heterophylla, Larix occidentalis, Picea engelmannii, Pinus contorta*
Picea sitchensis	*Larix occidentalis, Picea engelmannii*	*Thuja plicata*	*Pseudotsuga menziesii, Picea glauca*	*Thuja plicata, Pinus monticola, Abies lasiocarpa*
Alnus rubra		*Tsuga heterophylla*		

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[1] Compiled from information published by Fisher (1935), Taylor (1935), Godman (1953a), Bever (1954), Muri (1955), Smith (1955), Day (1957), Smith and Clark (1960), Jablanczy (1963), Soos and Walters (1963), Ruth (1968b), Boyd and Deitschman (1969), Schmidt (1969), Phelps (1973), and Ryker (1975). Species in upper groups are better suited to the seedbed than those in the lower groups. Data are insufficient for species comparisons within groups.

and vermiculite substracts in petri dishes. When Fisher (1935) compared germination on various seedbeds, he found that *Pseudotsuga menziesii*, *Abies grandis*, and *Pinus ponderosa* all germinated best on ash. *Tsuga heterophylla*, *Thuja plicata*, and *Larix occidentalis* germinated best on virgin *Pinus monticola* duff; but both *Picea engelmannii* and *Pinus contorta* germination were best on rotten wood.

Picea engelmannii duff proved to be lethal when Daniel and Schmidt (1972) stratified *P. engelmannii*, *Abies lasiocarpa*, *Pseudotsuga menziesii*, and *Pinus contorta* seeds in it. The lethal effect was eliminated by autoclaving, and it was much less severe when duff from other species was tested--*Pseudotsuga menziesii* and *Abies lasiocarpa* duff seriously affected only *P. menziesii* and *A. lasiocarpa* seeds, respectively; and *Pinus contorta* duff was almost neutral to seeds of all species. Moist *Tsuga heterophylla* duff delayed the germination of *Pseudotsuga menziesii* more than *Picea sitchensis*, *Pinus contorta*, *Tsuga heterophylla*, *Thuja plicata*, and *Abies amabilis* germination (Minore 1972). In a growth chamber experiment, Minore found that *P. menziesii* seedling survival was better on rotten *P. menziesii* wood than on *Tsuga heterophylla* duff but *Alnus rubra* survival was better on the duff. Failure to develop either root hairs or root nodules on the rotten wood probably contributed to *A. rubra*'s poor survival there.

Alnus rubra survival and growth seem to be better on mineral soil than on organic seedbeds. As *Tsuga heterophylla* and *Picea sitchensis* readily germinate and grow on organic seedbeds, reduced disturbance of the forest floor may favor these conifers over *A. rubra* in coastal Oregon and Washington (Ruth 1968b). In coastal Alaska and British Columbia, *Tsuga heterophylla* seems to be better suited to organic seedbeds than either *Picea sitchensis* (Taylor 1935, Day 1957) or *Thuja plicata* (Day 1957).

Farther inland, an undisturbed forest floor favors *Pseudotsuga menziesii* and *Abies lasiocarpa* over *Larix occidentalis* and *Picea engelmannii* but a mineral soil seedbed favors the *Larix* and *Picea* over *P. menziesii*, *A. lasiocarpa*, and *Pinus contorta* (Schmidt 1969). Although a mineral soil seedbed does not seem to be as critical for *P. menziesii* on some habitats as for other species, such as *Larix occidentalis* in the Rocky Mountains (Ryker 1975), Prochnau (1963) found that preparation of a mineral soil seedbed was essential to good establishment of *Picea glauca*, *Abies lasiocarpa*, *Pseudotsuga menziesii* and *Pinus contorta* in the central interior of British Columbia. Where a mineral soil seedbed was not prepared, *A. lasiocarpa* was able to establish itself better than *P. engelmannii* on litter and moss seedbeds (Smith 1955). *A. lasiocarpa* also seemed to be better than a *Picea engelmannii*-*P. glauca* hybrid in this respect...but the hybrid was more successful on rotten wood (Day 1964). Bulldozer scarification produces a seedbed more favorable for *P. engelmannii* than for *A. lasiocarpa* (Boyd and Deitschmann 1969).

Burned seedbeds also favor *P. engelmannii* over *A. lasiocarpa* (Muri 1955, Smith and Clark 1960). Although unburned mineral soil was more favorable for *Thuja plicata*, burned mineral soil was the best *Tsuga heterophylla* seedbed in British Columbia (Soos and Walters 1963). In central western Oregon, stocking of *Pseudotsuga menziesii* seedlings was better where slash was burned than where it was not. *Tsuga heterophylla* stocking showed no such difference (Bever 1954).

PHYSICAL CHARACTERISTICS

Unfortunately, burned seedbeds often result from fires that burn standing trees as well as slash. Northwestern tree species differ with respect to fire resistance and other physical characteristics. Many of these differences are summarized in table 18.

Anatomical differences among northwestern tree species are evident even in young seedlings. Cotyledon numbers vary, but they range within characteristic limits for most northwestern trees. Franklin (1961) noted these ranges in his seedling identification guide. *Pinus* species tend to have the most numerous cotyledons. "Cedars" (*Thuja, Chamaecyparis, Libocedrus* spp.) and *Taxus brevifolia* have the fewest.

NEEDLES

Smith (1970) used larger trees in determining needle volumes, weights, and longevity for several northwestern species. His data indicate that *Pinus monticola* needles are less dense than *P. contorta* needles when density is expressed as weight per unit volume. *Pseudotsuga menziesii* and *Picea sitchensis* needles also are less dense than those of *Pinus contorta* when weight-volume relationships are considered. When weight per unit surface area is the parameter being considered, *Pseudotsuga menziesii* is less dense than either *Pinus contorta* (Mellor and Tregunna 1972) or *Picea sitchensis* (Krueger and Ruth 1969). The weight-surface area measurements of Krueger and Ruth indicate that *Tsuga heterophylla* needles are less dense than *Pseudotsuga menziesii* needles, and *Alnus rubra* leaves are even less dense than *T. heterophylla*. Regardless of individual needle densities, *Tsuga heterophylla* and the *Pinus* species tend to lose their needles sooner than the *Picea* and *Abies* species (Smith 1970). Young *Pinus ponderosa* needles have higher levels of photosynthesis than young *Abies concolor* needles, but these levels decline faster with age in *P. ponderosa* (Freeland 1952).

Numbers and distribution of needles probably are as important as individual needle densities and photosynthetic levels in the life of a tree. Northwestern tree species exhibit characteristic differences in this respect, both in needle quantity and in aerial distribution. For example, *Pinus contorta* had 10 times the needle weight of *Picea glauca* and 6 times the needle weight of *Abies lasiocarpa* when 5-year-old seedlings were compared in British Columbia (Eis 1970). When total crown weights (branchwood as well as needles) of older trees are com-

CROWNS

Pinus ponderosa had the heaviest crown weight of 11 Rocky Mountain conifers compared by Brown (1976). Chandler (1960) also found *P. ponderosa* crown weight to be the heaviest when he calculated slash dry weights for large trees in the westside mixed conifer forests of California. For small trees, his calculations showed *Pseudotsuga menziesii* and *Abies concolor* crowns to be heavier than those of *P. ponderosa*. The crown weight of *Libocedrus decurrens* was the lightest calculated by Chandler; but *Larix occidentalis* and *Pinus monticola* had the lightest crowns measured by Brown. *Pinus contorta* crowns also are relatively light, and Tackle (1959) observed that *P. contorta* had a greater leaf area per unit of weight than *P. ponderosa*. Hardwood crown weights were not compared with these conifers, but Sundahl (1966) found *Lithocarpus densiflora* crowns to be about three times heavier than the crowns of *Arbutus menziesii* and two times heavier than those of *Quercus kelloggii*.

Species with heavy crowns tend to have larger crowns than species with light crowns, but crown shapes vary almost as much as crown weights. *Picea engelmannii* (Starker 1934, Fahnestock 1960) and *Abies lasiocarpa* (Flint 1925) have the longest crowns. Although Flint, Starker, and Fahnestock all rate *Larix occidentalis* as one of the shortest-crowned species, these authors differ with regard to other species. *Pinus monticola's* branch height is described as similar to that of *Larix occidentalis* ("high") by Flint (1925) and Starker (1934), but Fahnestock (1960) described *P. monticola* crowns as "medium to long" and listed *Larix occidentalis, Pinus ponderosa,* and *Pseudotsuga menziesii* in the "short to medium" crown category. The *P. menziesii* crown was described as being longer than that of *P. ponderosa* by Flint (1925), shorter than *P. ponderosa* by Starker (1934). Differences like these probably were caused by unrecognized environmental and stand density differences among observers. They have been resolved by listing species in the same

Table 18--Comparative physical characteristics

Cotyledon number[2]	Needle longevity[3]	Needle volume[3]	Needle weight[3]	Total crown weight[4]
Pinus lambertiana	*Abies grandis*	*Pinus monticola*	*Pinus contorta*	*Pinus ponderosa*
Pinus jeffreyi	*Picea sitchensis*	*Pinus contorta*	*Pinus monticola*	*Abies grandis, A. concolor, A. lasiocarpa, Pseudotsuga menziesii, Picea engelmannii*
Pinus ponderosa	*Abies amabilis*	*Abies grandis*	*Abies grandis*	*Tsuga heterophylla, Thuja plicata, Pinus contorta, P. albicaulis, P. lambertiana*
Pinus monticola	*Pseudotsuga menziesii*	*Picea sitchensis*	*Picea sitchensis*	*Larix occidentalis, Pinus monticola, Libocedrus decurrens*
Pinus attenuata, Pseudotsuga menziesii, Abies magnifica var. *shastensis, A. concolor*	*Pinus monticola*	*Pseudotsuga menziesii*	*Abies amabilis*	
Picea engelmannii	*Tsuga heterophylla*	*Tsuga heterophylla*	*Pseudotsuga menziesii*	
Abies amabilis, A. grandis, Larix occidentalis, Picea breweriana	*Pinus ponderosa*		*Tsuga heterophylla*	
Pinus contorta	*Pinus contorta*			
Picea sitchensis, Abies procera				
Abies lasiocarpa				
Tsuga mertensiana				
Tsuga heterophylla				
Chamaecyparis nootkatensis, C. lawsoniana, Thuja plicata, Taxus brevifolia, Libocedrus decurrens				

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[1] Species in the same group are not necessarily equal, but data are insufficient for species comparisons within groups.

[2] Compiled from data published by Franklin (1961). Species with many cotyledons are listed above those with few.

[3] Based on data published by Smith (1970). Species with the largest, heaviest, and most persistent needles are listed above those with smaller, lighter, and shorter-lived needles.

[4]

of northwestern tree species[1] (continued)

Crown length[5]	Crown width[6]	Crown density[7]	Annual litter fall[8]	Heartwood specific gravity[9]
Picea engelmannii, Abies lasiocarpa	*Pinus ponderosa, Tsuga heterophylla*	*Pinus albicaulis*	*Thuja plicata*	*Quercus garryana*
Tsuga heterophylla, T. mertensiana, Thuja plicata, Abies grandis, A. concolor	*Thuja plicata*	*Abies lasiocarpa*	*Pseudotsuga menziesii* (350 years old)	*Taxus brevifolia*
Picea sitchensis, Pinus ponderosa, P. contorta, Pseudotsuga menziesii, Abies procera, Pinus monticola	*Pseudotsuga menziesii*	*Picea engelmannii*	*Abies amabilis*	*Larix occidentalis*
Larix occidentalis	*Abies grandis*	*Abies grandis, Tsuga heterophylla, Pseudotsuga menziesii, Pinus ponderosa, P. contorta, P. monticola*	*Acer macrophyllum*	*Fraxinus oregona*
	Picea engelmannii	*Larix occidentalis*	*Pinus monticola*	*Pseudotsuga menziesii* var. *menziesii*
	Pinus monticola, P. contorta, Larix occidentalis	*Thuja plicata*	*Alnus rubra*	*Acer macrophyllum*
			Tsuga heterophylla	*Tsuga mertensiana*
			Pseudotsuga menziesii (100 years old)	*Pseudotsuga menziesii* var. *glauca, Sequoia sempervirens, Chamaecyparis lawsoniana*
			Picea sitchensis	*Tsuga heterophylla, Pinus contorta, P. ponderosa*
			Pinus ponderosa	*Picea sitchensis, P. glauca, Pinus jeffreyi, P. monticola, P. lambertiana, Abies magnifica, A. concolor, A. grandis, A. procera, A. amabilis, Alnus rubra, Populus tremuloides, Libocedrus decurrens*
			Pinus contorta	*Populus trichocarpa, Picea engelmannii, Abies lasiocarpa, Thuja plicata*

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[5] From Flint (1925), Starker (1934), and Fahnestock (1960). Species with long crowns are listed above those with shorter crowns.

[6] From Fahnestock (1960). Species with wide crowns are listed above those with narrow crowns.

[7] From Brown's (1978) measurements of foliage plus branchwood bulk densities in dominant trees. Species with dense crowns are listed above those with less-dense crowns.

[8] From Tarrant et al. (1951). The heaviest litter fall is listed at the top, the lightest at the bottom.

[9] Compiled from data published by Markwardt (1931), Markwardt and Wilson (1935), USDA Forest Products Laboratory (1955, 1965), Born (1966), and Farr (1973). Species with high specific gravities are listed above those with low specific gravities.

Table 18--Comparative physical characteristics

Branchwood specific gravity[10]	Sapwood thickness[11]	Bark thickness[12]	Foliage flammability[13]	Epiphyte receptivity[14]
Pseudotsuga menziesii	*Pinus ponderosa*	*Larix occidentalis, Pseudotsuga menziesii*	*Picea engelmannii, P. sitchensis, Pseudotsuga menziesii, Thuja plicata, Tsuga heterophylla, T. mertensiana, Abies procera, A. lasiocarpa*	*Alnus rubra*
Pinus contorta	*Pinus contorta*	*Pinus ponderosa*	*Abies grandis, A. concolor, Pinus monticola*	*Picea sitchensis, Abies procera*
Abies grandis, Larix occidentalis	*Pseudotsuga menziesii, Picea engelmannii*	*Abies grandis, A. concolor, A. procera*	*Pinus contorta*	*Tsuga heterophylla, Picea engelmannii*
	Thuja plicata	*Pinus monticola, Tsuga heterophylla, T. mertensiana*	*Larix occidentalis, Pinus ponderosa*	*Pseudotsuga menziesii, Larix occidentalis*
	Larix occidentalis	*Thuja plicata*		*Pinus monticola*
		Picea sitchensis, P. engelmannii, Pinus contorta, Abies lasiocarpa, Chamaecyparis nootkatensis		*Thuja plicata*
				Populus trichocarpa
				Acer macrophyllum
				Chamaecyparis nootkatensis, Taxus brevifolia
				Abies lasiocarpa
				Abies grandis, A. concolor
				Populus tremuloides
				Pinus contorta
				Quercus garryana
				Arbutus menziesii
				Tsuga mertensiana

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[10] From Ryan and Pickford (1978). Species with high specific gravities are listed above those with low specific gravities.

[11] From Lassen and Okkonen (1969). Species with thick sapwood are listed above those with thin sapwood.

[12] Compiled from information published by Flint (1925), Starker (1934), and Bones (1962). Species with thick bark are listed above those with thin bark.

[13] Compiled from information published by Flint (1925) and Starker (1934). Species with highly flammable foliage are listed above those with less flammable foliage.

[14] Compiled from information published by Flint (1925), Starker (1934), Coleman et al. (1956), and Pechanec and Franklin (1968). Species supporting more epiphytes are listed above those supporting less.

of northwestern tree species[1]

Fire resistance[15]		Rooting depth[16]	Windthrow resistance[17]	Growth in dense soils[18]	Snow damage resistance19
Coastal	Interior				
Pseudotsuga menziesii	*Larix occidentalis*	*Pinus ponderosa*	*Pseudotsuga menziesii, Thuja plicata*	*Larix occidentalis, Pinus monticola, P. ponderosa, P. lambertiana*	*Tsuga mertensiana, T. heterophylla, Picea breweriana, Abies magnifica* var. *shastensis*
Abies grandis, A. concolor	*Pinus ponderosa, Pseudotsuga menziesii*	*Pinus lambertiana, Libocedrus decurrens*	*Picea sitchensis*	*Pseudotsuga menziesii, Pinus contorta*	*Pinus monticola, Abies amabilis*
Tsuga mertensiana	*Pinus lambertiana, Abies grandis, A. concolor*	*Pseudotsuga menziesii, Abies grandis, Pinus monticola, Larix occidentalis*	*Tsuga heterophylla*	*Abies amabilis*	*Abies procera, A. concolor, Pinus jeffreyi*
Abies procera	*Libocedrus decurrens, Pinus monticola, Thuja plicata, Tsuga mertensiana*	*Thuja plicata*	*Abies amabilis*	*Picea sitchensis, Tsuga heterophylla, Thuja plicata*	*Pseudotsuga menziesii, Pinus lambertiana, P. ponderosa*
Pinus monticola	*Pinus contorta, Picea engelmannii, Tsuga heterophylla*	*Tsuga heterophylla*			
Pinus contorta	*Abies lasiocarpa*				
Tsuga heterophylla					
Picea sitchensis, Thuja plicata					

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[15] Based upon observations by Kerr (1913), Flint (1925), Starker (1934), Boyd (1959), Tackle (1959), and Wallis et al. (1974). Fire resistant species are listed above less resistant species.

[16] From Haig (1936) and Stein (1963). Deep-rooted species are listed above shallow-rooted species.

[17] From Boyce (1929), Ruth and Yoder (1953), and Gratkowski (1956). Resistant species are listed above non-resistant species.

[18] From Leaphart (1958), Stephens (1965), and Minore et al. (1969). Species capable of growing in dense soils are listed above those that are not.

[19] From Williams (1966), Kangur (1973), and Waring et al. (1975). Resistant species are listed above non-resistant species.

Conflicting references are not a problem with crown widths and crown densities, for there seem to be very few sources of this information. Fahnestock (1960) described *Pinus ponderosa* and *Tsuga heterophylla* crowns as "wide;" *Pinus monticola, P. contorta,* and *Larix occidentalis* crowns as "narrow." His intermediate descriptions were used in ranking crown widths in table 18. Brown's (1978) measurements of foliage and branchwood bulk densities were used in ranking crown densities. Although he did not rank species in terms of crown width or density, Gratkowski (1956) noted that *Thuja plicata* crowns were less dense than the crowns of *Tsuga heterophylla* and *Abies amabilis*. Fahnestock (1960) observed that the quantity of foliage plus very fine twigs in individual crowns seems to be related to species shade tolerance--the higher the percentage of total crown weight in foliage, the more tolerant is the species.

LITTER FALL

Large, dense crowns do not necessarily produce large quantities of litter. When Tarrant et al. (1951) measured the annual litter fall in pure, well-stocked stands of 10 northwestern tree species, they found that *Thuja plicata* (a species with moderate crown size and density) produced the most litter. A 350-year-old stand of *Pseudotsuga menziesii* dropped more than twice as much litter as a 100-year-old stand, and age differences may have influenced the data published by Tarrant et al. Nevertheless, their general comparison emphasizes the large differences between species...*Thuja plicata* produced almost eight times as much litter as *Pinus contorta*.

WOOD

Although they may not vary annually like litter fall, wood properties of the various species are not at all constant. They vary with latitude, age, and position in the tree. Nevertheless, differences in wood characteristics among species are of great importance and have been studied extensively. Most of these studies will not be reviewed here. Only two wood properties have been selected for comparison--heartwood specific gravity and sapwood thickness.

Specific gravity values were compared to obtain the species ranking shown in table 18. Not shown are species differences in the way wood specific gravity changes with height in the tree. Okkonen et al. (1972) found that specific gravity decreased as height increased in *Pseudotsuga menziesii, Pinus ponderosa, Larix occidentalis, Abies grandis, A. procera, A. magnifica,* and *A. amabilis*. It increased with height in *Thuja plicata, Populus trichocarpa,* and *Picea engelmannii*. The specific gravity of *Abies concolor* initially decreased, then increased farther up the tree. Progressing outward from pith to bark, tracheid length tends to increase in all conifers--but Anderson's (1951) four-tree sample indicated that this increase is greater in *Pseudotsuga menziesii* than in *Abies concolor* or *A. procera*.

Sapwood thickness increases with increasing tree diameter in western softwoods (Lassen and Okkonen 1969). When Grier and Waring (1974) compared sapwood cross sectional area and foliage mass, they found them to be highly correlated. Furthermore, the correlations varied consistently among the three species investigated. *Pseudotsuga menziesii* had more foliage per unit sapwood than either *Abies procera* or *Pinus ponderosa*. In small trees, *P. ponderosa* had more foliage per unit sapwood than *A. procera,* but in large trees *A. procera* had more foliage for its sapwood than *P. ponderosa*.

The pattern of water conduction in sapwood and heartwood differs among northwestern conifers. It occurs in an ascending right spiral in *Pinus contorta, P. ponderosa, P. jeffreyi, Larix* species, *Picea* species, and *Abies* species (Rudinsky and Vite' 1959). In *Pinus monticola* and *P. lambertiana,* conduction occurs in an ascending left spiral. Rudinsky and Vite' discovered an interlocking zigzag ascent in *Libocedrus decurrens*, *Sequoia sempervirens*, and *Juniperus* species. In *Pseudotsuga menziesii* and *Tsuga* species, the ascent of water is neither in a complete spiral nor along an interlocking pathway--it winds around the stem in a coherent section. The coherent section does not wind in *Thuja plicata* and *Chamaecyparis lawsoniana*, but goes straight up the tree. Pattern of water conduction probably influences sapwood permeability. *Pseudotsuga menziesii* sapwood is less permeable than that of *Pinus contorta* or *Picea engelmannii* (Markstrom and Hann 1972). In contrast, heartwood permeability to liquids is higher in *P. engelmannii* and *P. menziesii* than in *P. contorta;* permeability to gases is higher in *P. contorta.*

BARK

Bark characteristics are more easily seen and compared than most physical attributes. As a result, bark traits tend to be general knowledge, and only a few comparisons of bark thickness have been published. These are very similar, ranking in the order shown in table 18. As the comparative bark thicknesses indicate, total bark content of the tree is higher for *Pseudotsuga menziesii* than for either *Tsuga heterophylla* or *Thuja plicata* (Smith, Kerr, and Czizmazia 1961). Relatively thin bark and a long cylindrical bole give *Abies procera* a greater volume for its diameter at breast height than associated species, with the possible exception of *Pinus monticola* (Hanzlik 1925).

Resin content of old bark was characterized in general terms by Flint (1925). *Pinus ponderosa*, *P. contorta*, and *P. monticola* barks have the most resin; *Larix occidentalis*, *Abies grandis*, *Tsuga heterophylla*, *T. mertensiana*, and *Thuja plicata* barks have the least. Flint rated *Pseudotsuga menziesii*, *Picea engelmannii*, and *Abies lasiocarpa* as intermediate in bark resin content.

SLASH

Bark resin content is an important determinant of fire intensity. So are the slash characteristics and foliage inflammability of northwestern tree species. Foulger et al. (1976) analyzed western softwood logging residues less than .25 inch (.64 cm) in diameter for bark, needle, and solid wood content. They found that *Larix occidentalis* had the highest proportion of solid wood, followed by *Pinus contorta*, *Pseudotsuga menziesii*, *Abies concolor*, *A. lasiocarpa*, *Pinus ponderosa*, and *Picea engelmannii*. Moisture content of the solid wood component of slash also may differ in different species, sometimes in unexpected ways. Scott (1964) found that moisture distribution in large-diameter *Pseudotsuga menziesii* slash was radial, with moisture content increasing from 6 in (15 cm) inside the log out to its surface. The moisture distribution in large *Lithocarpus densiflora* slash on the same clearcut was just the opposite, however, with moisture content decreasing from inside out.

Moisture distribution, branch size, and needle retention all effect the flammability of slash. Olson (1953) made some preliminary tests of slash flammability in the western white pine type. He concluded that fire spread rates were highest in *Larix occidentalis* slash until it lost its needles, followed by *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Pinus monticola*, *Abies grandis*, *Pinus contorta*, *Thuja plicata*, *Picea engelmannii*, and *Pinus ponderosa*. Although it had the slowest spread rate, *P. ponderosa* had the hottest-burning slash. Fahnestock (1960) tested slash quality more extensively. He suggested the following spread-rate rankings:

Fresh Slash

Larix occidentalis (fastest spread)

Pinus monticola, *Thuja plicata*, *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Abies grandis* (intermediate spread)

Pinus ponderosa and *Picea engelmannii* (slowest spread)

One-year-old Slash

Pinus monticola, P. contorta, Thuja plicata (fastest spread)

Pinus ponderosa, Pseudotsuga menziesii, Tsuga heterophylla, and *Picea engelmannii* (intermediate spread)

Abies grandis and *Larix occidentalis* (slowest spread)

Fahnestock found needle moisture content in fresh slash to be highest in *Larix occidentalis,* lowest in *Pseudotsuga menziesii.* Branchwood moisture in freshly cut slash was highest in *Pinus contorta,* lowest in *Larix occidentalis.*

MOISTURE CONTENT

Moisture content apparently differs in standing trees as well as in slash. Parker (1954) measured more heartwood moisture and total trunk water content in *Pinus ponderosa* and *Abies grandis* than in *Pseudotsuga menziesii* or *Thuja plicata.* When he compared twig moisture content with the foliage weight attached to those twigs, he found that *Pinus ponderosa* also had far more water per unit foliage than *Abies grandis, Pseudotsuga menziesii,* or *Thuja plicata.* The seasonal fluctuation of foliage moisture content was studied by Pharis (1967), who noted that the summer moisture content of new foliage was higher in *Pinus ponderosa* and *P. lambertiana* than in *Pseudotsuga menziesii.* Foliage moisture content declined between November and February in *P. menziesii* and *Abies grandis,* but not in *P. lambertiana, P. ponderosa,* or *Libocedrus decurrens.*

FOLIAGE FLAMMABILITY AND EPIPHYTE RECEPTIVITY

Foliage moisture probably influences foliage flammability, a factor rated by Flint (1925) in the northern Rocky Mountains and by Starker (1934) in Oregon and Washington. As their species comparisons were quite similar, they were combined in table 18 with only minor modification. Both authors listed relative quantity of lichen growth by tree species. Coleman et al. (1956) studied the growth of lichens and other epiphytes more intensively, ranking Olympic Peninsula tree species in terms of epiphyte receptivity. They found *Alnus rubra* to be the best epiphyte host, *Tsuga mertensiana* to be the worst host on the Olympic Peninsula of Washington. In Oregon, Pechanec and Franklin (1968) found *A. rubra* to be a better epiphyte host than either *Picea sitchensis* or *Pseudotsuga menziesii.*

FIRE RESISTANCE

Bark characteristics, foliage flammability, and epiphyte populations all contribute to the total flammability of northwestern tree species. This whole-tree flammability and relative species resistance to fire have been compared by several authors. In the interior, Tackle (1959) observed that *Pinus contorta* was more susceptible to fire than other *Pinus* species or *Pseudotsuga menziesii,* but was less susceptible than *Picea engelmannii* and *Abies lasiocarpa.* Kerr (1913) also found that *P. contorta* was more fire-susceptible than *P. ponderosa.* Flint (1925) compared the fire resistance of 11 northern Rocky Mountain conifers, finding *Larix occidentalis* to be most resistant and *Abies lasiocarpa* least resistant. He noted that intolerant trees of the northern Rocky Mountains tend to be highly fire-resistant, while tolerant ones tend to have low resistance.

Relative species fire resistance does not appear to be the same in coastal forests as it is farther inland. *Thuja plicata* is more severely damaged by fire than any of its associates along the coast, but is less susceptible than *Picea engelmannii, Tsuga heterophylla,* and *Abies lasiocarpa* in the Inland Empire (Boyd 1959). Therefore, the fire resistance ranking in table 18 was divided into coastal and interior portions. *Pseudotsuga menziesii* seems to be the most fire-resistant coastal species (Starker 1934). Starker listed *Picea sitchensis* as the least fire resistant of 13 Oregon and Washington trees. Farther south, Stone and Vasey (1968) compared the e resistance of *Sequoia semper-* *ens* and its associates, noting t both *S. sempervirens* and *ocarpus densiflora* are more e-resistant than *P. menziesii* *Abies grandis*.

In the north, a survey of fire-led timber on a burn in British umbia showed that 50 percent of *Thuja plicata*, but only 20 per- t of the *Tsuga heterophylla* and y 1 percent of the *Pseudotsuga* *ziesii* trees were charred enough degrade mill quality (Wallis, frey, and Richmond 1974). When aughton (1944) studied charring the ignition temperatures of d, he found that speed of ignition directly correlated with wood cific gravity. Species with low cific gravity (e.g., *Picea* *chensis*) ignited before species h high specific gravity (e.g., *ix occidentalis*).

TS

Root charring commonly occurs ing severe forest fires, and cies rooting characteristics bably are significant determinants fire resistance. Young *Pinus* *derosa* roots grow deeper than *Lambertiana* and *Libocedrus decur-* *s* roots, and the young *P.* *bertiana* and *L. decurrens* roots d to be deeper than *Abies grandis* *Pseudotsuga menziesii* roots of same age (Stein 1963). *Thuja* *cata* roots are even shallower n those of *A. grandis* and *P.* *ziesii* (Ross 1932). *Tsuga hetero-* *lla* seedling roots are shallower n the seedling roots of *Abies* *bilis* (Scott et al. n.d.). Indeed, *ga heterophylla* roots seem to be shallowest of all (Haig 1936, ch 1964). Although not compared ectly with the above species, *es lasiocarpa* and *Picea glauca* arently also have shallow roots--llower than *Pinus contorta* (Eis 0). *Pinus contorta* tends to be e shallow-rooted than *P. pon-* *osa* (Gail and Long 1935, Tarrant 3).

Lateral extent, structure, and position of species root systems y even more than depth. *Populus* *muloides* probably has the greatest eral root extent (Berndt and Gibbons 1958). *Picea glauca* roots spread laterally more than *Abies lasiocarpa* roots, and *A. lasiocarpa* root systems spread more than those of *Pinus contorta* when root spread was considered in relation to tree height (Eis 1970). When root spread was related to crown width in root spread/crown width ratios, species were ranked as follows (Smith 1964):

Pinus contorta (highest ratio)
Picea sitchensis
Pinus ponderosa
Pseudotsuga menziesii
Tsuga heterophylla
Thuja plicata
Alnus rubra (lowest ratio)

As crown widths of these species differ (table 18), absolute root spread may not always be greater in species with higher root spread/crown width ratios. For example, roots of the wide-crowned *Pinus ponderosa* actually spread more laterally than those of the narrow-crowned *P. contorta* (Tarrant 1953). Nevertheless, *Pseudotsuga menziesii* root spread is wider than that of either *Tsuga heterophylla* or *Thuja plicata* when considered on an absolute basis (Eis 1974). Absolute measurements of the total root masses of windthrown trees of four species (Steinbrenner and Gessel 1956) showed *Pseudotsuga menziesii* to have the most extensive root system, followed in descending order by *Abies procera*, *Tsuga heterophylla*, and *Thuja plicata*.

When *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata* root distribution and structure are considered further, other differences become evident. *T. plicata* roots are more numerous in the duff than in underlying soil where a heavy duff layer exists (Ross 1932). Ross found that *T. heterophylla* root tips were also present in this duff, but not to the same extent. He found very few *P. menziesii* feeding roots in the duff layer...they were deeper, in the underlying soil. Ross also observed that *T. heterophylla* roots were smaller than those of *P. menziesii*, tending to be more oval in cross section than the circular *Pseudotsuga* roots.

Eis (1974) observed larger root diameters in *Pseudotsuga menziesii* than in either *Tsuga heterophylla* or *Thuja plicata*. After hydraulic excavation, he found that thin, rope-like roots were most dense on *T. plicata* trees, least dense on *P. menziesii*. In an earlier study Eis (1972) noted that root grafting occurred in all three species, but was most frequent in *T. plicata*, least frequent in *P. menziesii*. The grafts apparently were important aids to the survival of suppressed trees on Vancouver Island.

Farther inland, Eis (1970) studied root growth relationships of juvenile trees in interior British Columbia. For the same age, *Pinus contorta* root systems were denser than those of either *Picea glauca* or *Abies lasiocarpa*. Vertical "sinker" roots were more numerous in *P. contorta*. Its roots were more branched than those of *Picea glauca*. In western Montana, Wyoming, and Idaho, Gail and Long (1935) also studied the rooting relationships of *Pinus contorta* and its associates. They found that *P. contorta* lateral roots grew more horizontal and closer to the soil surface than those of *P. ponderosa*.

The root systems of *Pseudotsuga menziesii* var. *glauca*, *Abies grandis*, *Larix occidentalis*, *Pinus monticola*, and *Thuja plicata* grown in large containers were investigated by Leaphart and Wicker (1966). They found the best taproot development in *L. occidentalis*, followed by *P. menziesii* and *A. grandis*. Taproots in *T. plicata* and *P. monticola* were poorly defined. Fine roots apparently varied inversely with taproot development for *T. plicata* had the most profusely developed fine root system, and *L. occidentalis* had the least profuse system.

Root system strength is a crucial factor in maintaining the stability of steep forested slopes. Burroughs and Thomas (1977) compared the tensile strength of *Pseudotsuga menziesii* var. *menziesii* and *P. mensiesii* var. *glauca* roots, finding var. *menziesii* roots to be stronger when fresh. In similar studies, Ziemer and Swanston (1977) found live *Tsuga heterophylla* roots to be stronger than live *Picea sitchensis* roots. O'Laughlin (1973) found no significant difference in tensile strengths of *Pseudotsuga menziesii* and *Thuja plicata* roots.

WINDTHROW RESISTANCE

Root strength, depth, and structure affect the windthrow resistance of northwestern tree species--resistance that has been compared in several publications. The New Zealand Forest Service (1976) rated *Pseudotsuga menziesii* as more windfirm than most other conifers. Steinbrenner and Gessel (1956) also rated *P. menziesii* as most resistant, followed in order by *Abies procera*, *Tsuga heterophylla*, and *Thuja plicata*. Their *P. menziesii-T. heterophylla* comparison, based on large samples, is more reliable than their *A. procera* and *T. plicata* rankings, which were based on observations of only two and seven trees, respectively. When Gratkowski (1956) analyzed windthrow by comparing species composition of the stand with species composition of the windthrown trees, he found that short *Thuja plicata* trees growing on dry sites were most resistant, followed by *Pseudotsuga menziesii*, *Tsuga heterophylla*, and (least resistant) *Abies amabilis*. Boyd (1959) tentatively rated *Thuja plicata* fourth in Inland Empire windfirmness, exceeded by *Larix occidentalis*, *Pinus ponderosa*, and *Pseudotsuga menziesii*. Boyce (1929) found both *T. plicata* and *P. menziesii* to be more resistant to windthrow than *Tsuga heterophylla*, *Abies amabilis*, or *Picea sitchensis* on the Olympic Peninsula. In the Oregon Coast Range, *P. sitchensis* is more windfirm than *T. heterophylla* (Ruth and Yoder 1953).

DENSE SOIL TOLERANCE

Soils interact with species characteristics in determining windthrow resistance, and even a windthrow-resistant species may fare poorly on shallow or dense soils that limit root penetration and growth. Northwestern tree species differ with respect to their growth in dense soils, however--some are able to tolerate rather high soil densities, while others cannot.

On soils developed from Eocene to Miocene volcanic rocks in the western Cascade Range, clay subsoils restrict *Pseudotsuga menziesii*, but not *Pinus*

nderosa or *P. lambertiana* roots
tephens 1965). Cochran (1963)
ted longer lateral roots and
eater total root weights in *Pinus*
mbertiana than in *P. ponderosa*
ring the initial stages of seedling
velopment in high density soil.
il density was one of the param-
ers utilized by Forristall and
ssel (1955) in comparing the growth
Thuja plicata, Alnus rubra,
eudotsuga menziesii, and *Tsuga*
terophylla in Washington. Unfortu-
tely, their soil density-growth
mparisons probably were confounded
other factors, for the different
ecies grew on plots with differing
il textures and moisture contents.
A uniform soil was artificially
mpacted to different bulk densities
Minore, Smith, and Woollard (1969)
compare the effects of high soil
nsity on seedling root growth of
ven northwestern species. In
years, the roots of *Pinus contorta,*
eudotsuga menziesii, Alnus rubra,
d *Abies amabilis* penetrated soil
lumns that the roots of *Picea*
tchensis, Tsuga heterophylla, and
uja plicata did not. In another
udy, Leaphart (1958) found that
rix occidentalis and *Pinus monti-*
la roots penetrated hardpan layers
re effectively than the roots of
eudotsuga menziesii, Pinus con-
rta, Abies grandis, Picea engel-
nnii, Thuja plicata, or *Tsuga*
terophylla.

CHANICAL DAMAGE RESISTANCE

Soil compaction probably is not
ry important when seedlings are
ried by silt. Nevertheless,
rmann and Lavender (1967) ob-
rved less damage to *Pinus pon-*
rosa than to *Pseudotsuga*
nziesii when dormant seedlings
both species were buried under
lt for more than 8 weeks. Burial
der litter that accumulates on
p of the winter snow pack is
sisted better by *Abies amabilis*
an by *Tsuga heterophylla* seedlings
hornburg 1969).

Damage caused by the snow pack
self varies greatly among species
able 18). *Tsuga heterophylla,*
mertensiana, Picea breweriana,
d *Abies magnifica* var. *shastensis*
em most resistant to snow damage.
Pinus monticola and *Abies amabilis* are somewhat less resistant but able to tolerate snow weights better than *Abies concolor, A. procera,* or *Pinus jeffreyi* (Williams 1966, Waring et al. 1975). *Pseudotsuga menziesii, Pinus lambertiana,* and *P. ponderosa* seem to be most subject to snow damage of the species compared.

ANIMAL RELATIONSHIPS

Most animal damage in young stands seems to be caused by gophers, rabbits, or deer. No species comparisons are available for gopher damage, for available data indicate little or no species preference by these rodents. Differences in rabbit damage were noted by Worthington (1955), however, who found *Pseudotsuga menziesii* to be damaged more than *Thuja plicata* and *Tsuga heterophylla. Abies grandis* and *Picea sitchensis* were least damaged on Worthington's Olympic Peninsula sites. Staebler et al. (1954) also found *P. menziesii* to be more damaged by rabbits than *T. heterophylla.* The *Chamaecyparis lawsoniana* seedlings on their southwestern Washington plots were browsed by deer, but only after 3 years.

Schubert (1956) observed more deer browsing on *Abies concolor* than on *Pinus lambertiana,* and Stark (1965) found more browsing on *A. concolor* and *Libocedrus decurrens* than on *Pinus ponderosa* and *P. lambertiana. Abies magnifica* also seems to be less damaged by deer browsing than *A. concolor* (Gordon 1970). When both rabbit and deer damage are considered, comparative animal damage may be ranked by species groups:

Pinus ponderosa, P. lambertiana, Abies grandis, A. magnifica, and *Picea sitchensis* (least damaged)

Abies concolor, Libocedrus decurrens, and *Tsuga heterophylla*

Thuja plicata and *Chamaecyparis lawsoniana*

Pseudotsuga menziesii (most damaged)

Relative species palatability may influence relative species damage, but highly palatable species may not comprise the majority of an animal's diet. For example, *Thuja plicata* is a highly palatable, preferred deer food; but it occurred in only 20-30 percent of the deer stomachs sampled by Cowan (1945) on Vancouver Island, never amounting to more than 2 percent of the food volume. In contrast, *Pseudotsuga menziesii* occurred in 50-100 percent of Cowan's deer samples and accounted for 25-50 percent of their food volume.

Pseudotsuga menziesii seeds are eaten by rodents in preference to *Abies procera* seeds (Dick 1960). Small mammals and birds also seem to prefer *P. menziesii* seeds to the seeds of *Tsuga heterophylla* (Gashwiler 1970). They prefer *T. heterophylla* to *Thuja plicata* (Gashwiler 1967).

INSECT RESISTANCE

General insect resistance seems to be associated with species longevity. *Thuja plicata* is more insect-resistant than *Tsuga heterophylla* or *Abies amabilis* in coastal British Columbia (Schmidt 1955). It also is more resistant to insect attacks than most of its Inland Empire associates (Boyd 1959). *Thuja plicata* maintains this high insect-resistance rating when more limited insect categories are considered. It is attacked less by woodborers than *Pseudotsuga menziesii, Abies grandis,* or *Tsuga heterophylla* (Johnson 1958); and its extracts apparently induce more deaths in western tent caterpiller pupae than extracts of *P. menziesii* (Wellington 1969). *P. menziesii* is attacked by the silver-spotted tiger moth more often than *Thuja plicata, Tsuga heterophylla, Pinus contorta, Picea sitchensis, Abies amabilis,* and *A. grandis* in British Columbia (Sellars-St. Clare 1968). *Abies grandis* is damaged more than *P. menziesii* by western spruce budworm attacks, however, even when budworm egg numbers are similar in the upper crowns of these two species (Carolin and Coulter

The crowns of *Pinus lambertiana* and *P. monticola* seedlings were more seriously infested with woolly aphids than those of *P. albicaulis* when an accidental aphid infestation occurred during a lathhouse blister rust experiment (Hoff and McDonald 1977). Mitchell (1966), comparing *Abies* species in the field, observed that *A. concolor* and *A. procera* were most resistant to balsam woolly aphid. *Abies lasiocarpa* was least resistant (table 19).

Abies lasiocarpa also probably lacks resistance to termite attack, as do *Picea engelmannii, Tsuga heterophylla, Larix occidentalis,* and *Pseudotsuga menziesii.* Carter and Smythe (1974) found the woods of these species to be better termite food than the woods of *Thuja plicata, Sequoia sempervirens, Chamaecyparis lawsoniana,* and *Pinus ponderosa. Pinus ponderosa* apparently is cutworm resistant as well. When Fowells (1940) and Fowells and Stark (1965) tallied cutworm damage to seedlings in California, they found *Pinus lambertiana* to be least damaged, followed by *P. ponderosa* and *P. jeffreyi* (table 19). The cutworms showed a preference for *Libocedrus decurrens* over *Abies concolor* and the *Pinus* species.

Further comparisons of insect resistance among northwestern species are complicated by host specificity problems. Many serious insect pests attack only one or two tree species, and literature references to comparative species resistances are unavailable for them.

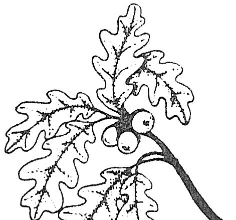


Table 19--Comparative insect resistance of northwestern tree species[1]

Cutworms[2]	Wood borers[3]	Termites[4]	Balsam woolly aphid[5]	Woolly aphid[6]
Pinus lambertiana	*Thuja plicata*	*Thuja plicata, Chamaecyparis lawsoniana, Sequoia sempervirens, Pinus ponderosa*	*Abies procera, A. concolor*	*Pinus albicaulis*
Pinus ponderosa, P. jeffreyi	*Pseudotsuga menziesii, Tsuga heterophylla, Abies grandis*	*Picea engelmanni, Tsuga heterophylla, Larix occidentalis*	*Abies magnifica* var. *shastensis*	*Pinus monticola*
Abies concolor		*Abies lasiocarpa, Pseudotsuga menziesii*	*Abies grandis*	*Pinus lambertiana*
Libocedrus decurrens			*Abies amabilis*	
			Abies lasiocarpa	

[1] Resistant species are listed above susceptible ones. Species in the same group are not necessarily equal, but data are insufficient for species comparisons within groups.

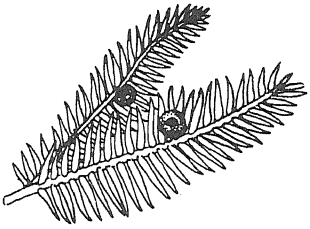
[2] From Fowells (1940) and Fowells and Stark (1965).

[3] From Johnson (1958).

[4] From Carter and Smythe (1974).

[5] From Mitchell (1966).

[6] From Hoff and McDonald (1977).



DISEASE RESISTANCE

Comparing disease resistance of northwestern tree species also is complicated by host specificity. Many pathogens, though widespread, are limited to a small number of host species. Other diseases consist of many pathogens attacking many trees, with each pathogenic species preferring a single tree species. The dwarf mistletoes are an example. Smith (1974) inoculated several tree species with several dwarf mistletoe species. He observed that each had a principal host on which it was particularly infectious, but they were not strictly host-specific. The greatest mistletoe seed retention occurred on the branches of *Picea engelmannii*, *P. sitchensis*, and *P. glauca*. The poorest occurred on *Pinus ponderosa* and *Larix occidentalis*. In contrast, the best mistletoe seed germination was on *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Abies grandis*; the poorest was on the *Picea* species.

Host specificity sometimes is evident within a single genus. For example, northwestern *Pinus* species exhibit some differential resistance to attack by rust fungi. *Pinus contorta* is more resistant to comandra rust than *P. ponderosa* (Bergdahl and French 1976). *P. monticola*, though susceptible, is less susceptible to white pine blister rust than other northwestern five-needled *Pinus* species. *Pinus albicaulis* is most susceptible and *P. lambertiana* is intermediate (Childs and Bedwell 1948).

Unfortunately, all northwestern *Pinus* species seem to be equally susceptible to annosus root rot (Bega 1962). In California they die soon after *Fomes annosus* invades and rapidly kills the cambium.

This does not happen in other California conifers. Instead, the fungus causes a chronic decay condition which the *Abies* species and other non-*Pinus* conifers appear to tolerate for several years (Bega and Smith 1966). *Pinus* species may be more tolerant in Britian than they are in California, for Aldhous and Low (1974) subjectively rated the pines as being more resistant than other conifers to *Fomes* butt rot. These other conifers do possess varying degrees of susceptibility to annosus root and butt rot, however, wherever they are grown (table 20). *Tsuga heterophylla* and *Picea sitchensis* are less resistant than *Abies grandis*, *A. procera*, and *Pseudotsuga menziesii* in Britian, where *Thuja plicata* is relatively susceptible (Aldhous and Low 1974). In British Columbia *Pseudotsuga menziesii* roots are more resistant than *Tsuga heterophylla* roots, and *Thuja plicata* stumps are more resistant to *Fomes* spore infection than the stumps of other conifer species (Wallis and Ginns 1968).

Tsuga heterophylla seedlings are more susceptible than *Pseudotsuga menziesii* seedlings to *Rhizina undulata*, a root pathogen that can be serious where slash has been burned (Morgan 1973).

Table 20--Comparative decay resistance of northwestern tree species[1]

Annosus root and butt rot[2]	Laminated root rot[3]	Decay in living trees[4]	Decay in dead wood[5]
Pseudotsuga menziesii, Abies procera, A. grandis	*Acer macrophyllum, Alnus rubra, Arbutus menziesii, Lithocarpus densiflora, Populus trichocarpa, P. tremuloides*	*Pinus ponderosa*	*Thuja plicata, Sequoia sempervirens, Taxus brevifolia*
Tsuga heterophylla, Picea sitchensis	*Libocedrus decurrens, Pinus ponderosa, Thuja plicata*	*Pinus monticola, P. lambertiana*	*Larix occidentalis*
	Pinus contorta, P. monticola	*Pinus contorta*	*Pseudotsuga menziesii*
	Abies lasiocarpa, Larix occidentalis, Picea engelmannii, P. sitchensis, Tsuga heterophylla	*Sequoia sempervirens*	*Pinus ponderosa, P. lambertiana, Picea sitchensis*
	Abies amabilis, A. grandis, Pseudotsuga menziesii, Tsuga mertensiana	*Picea sitchensis*	*Pinus monticola, P. contorta, Abies procera, A. concolor, A. amabilis, Tsuga heterophylla, Picea engelmannii*
		Pseudotsuga menziesii	
		Abies species	
		Tsuga heterophylla	

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[1] Resistant species are listed above susceptible ones. Species in the same group are not necessarily equal, but data are insufficient for species comparisons within groups.

[2] From Aldhous and Low (1974) and Wallis and Ginns (1968).

[3] From Hadfield and Johnson (undated).

[4] From Buckland et al. (1949), Wagener and Davidson (1954), and Farr et al. (1976).

[5] From Boyce (1929), Englerth and Scheffer (1954), USDA Forest Products

When Vaartaja (1957) germinated even northwestern tree species on gar cultures of a damping-off ungus (*Phytophthora cactorum*), he ound *Thuja plicata* to be much more esistant than *Larix laricina*, and *laricina* was more resistant than *cea glauca, P. mariana, P. sitchens, Pinus contorta*, or *P. ponderosa*.

Another fungus, the laminated oot rot caused by *Phellinus (Poria) eirii*, has been studied extensively. occurs on many northwestern pecies. *Thuja plicata, Alnus bra*, and *Acer macrophyllum* have ore resistance to this fungus han *Pseudotsuga menziesii* (Wallis d Reynolds 1967). *Phellinus* inected roots have profuse ectotrophic ycelium in *Pseudotsuga menziesii* d *Tsuga heterophylla*; limited ycelium in *Pinus monticola, P. ntorta*, and *P. ponderosa*; and most no mycelium in *Thuja plicata* Vallis 1976). Hadfield and Johnon (undated) compared host susceptibility in the summary publication sed as a source for the species omparisons listed in table 20.

Table 20 summarizes the general ecay information available in everal literature sources. Living *cea sitchensis* trees less than 0 years old are relatively free rot in southeastern Alaska; *uga heterophylla* trees are not arr et al. 1976). *Abies amabilis* ess than 350 years old on Vancouver sland also is more resistant to nfection by wood-rotting fungi han *Tsuga heterophylla* (Buckland al. 1949). When heart rot in *bies* species is compared with rot other genera, it is less prevalent han in *Tsuga*, but more prevalent han in *Pseudotsuga* or *Picea* Wagener and Davidson 1954). Within enera, Wagener and Davidson's data ndicate that living *Pinus ponderosa* as less heart rot than *P. monticola* d *P. lambertiana*.

Pinus ponderosa and *P. lambertiana* ere more decay-resistant than *P. nticola, P. contorta, Abies rocera, A. concolor, Tsuga heterohylla*, and *Picea engelmannii* when lark (1957) exposed heartwood amples to wood-rotting fungi in he laboratory. Clark found *Pseudosuga menziesii* heartwood to be ven more resistant than the *Pinus* pecies. In similar laboratory tests, Englerth and Scheffer (1954) found *Larix occidentalis* to be more decay-resistant than *Pseudotsuga menziesii* but less resistant than *Thuja plicata*. *Thuja plicata* was also found to be more decay-resistant than the wood of other species by Boyce (1929) and Wallis et al. (1974). Boyce, studying the deterioration of windthrown timber on the Olympic Peninsula, recorded more decay in *Abies amabilis* and *Tsuga heterophylla* than in *Picea sitchensis*, more in *P. sitchensis* than in *Pseudotsuga menziesii*.

When Childs (1939) studied the deterioration of slash on clearcut areas in the Douglas-fir region, he found the rate of sapwood decay to be about the same in *Pseudotsuga menziesii, Picea sitchensis*, and *Tsuga heterophylla* slash. *P. menziesii* heartwood decayed more slowly than the other two species, however, and heartwood decay in *Picea sitchensis* was slower than in *Tsuga heterophylla*. Similar reports were reported by Roff and Eades (1959) and by Ruth and Harris (1975). *Tsuga heterophylla* and *Abies amabilis* heartwood decay faster than the heartwoods of *Picea sitchensis* and *Pseudotsuga menziesii*. *Thuja plicata* is slowest to decay.

When root decay rates are compared, species ranking changes slightly. As one would expect, *Thuja plicata* roots lose their tensile strength more slowly than *Pseudotsuga menziesii* roots (O'Laughlin 1973). *Picea sitchensis* roots decay faster than *Tsuga heterophylla* roots in southeastern Alaska, however (Ziemer and Swanston 1977), reversing the relative heartwood decay rates of these two species.

CHEMICALS

Most chemically oriented species comparisons in the literature refer to chemical damage, not benefits. For example, smoke from slash burning apparently damages *Pseudotsuga menziesii* more than *Pinus lambertiana* or *P. ponderosa*, which are damaged more than *Libocedrus decurrens* or *Abies grandis* (Stein 1963). Nevertheless, some chemical effects are beneficial. Germination rates may be accelerated by applying hydrogen are benefitted more than *Abies lasiocarpa* by this treatment (Shearer and Tackle 1960). *P. menziesii* also benefits more than *Pinus lambertiana* or *P. ponderosa* when seeds are treated with hydrogen peroxide (Stein 1965).

HERBICIDES

Pseudotsuga menziesii is more resistant to injury by herbicides used in brush control than *Pinus ponderosa* (Newton 1963), and it is less damaged than *Alnus rubra* by dormant sprays (Gratkowski 1975). Brush control herbicides damage *Tsuga heterophylla* more than *Picea sitchensis* (Krygier and Ruth 1961). *T. heterophylla* also is damaged by weed-control herbicides. When Stewart (1977) tested 18 weed-control herbicides in forest nurseries, he found *T. heterophylla* and *Sequoia sempervirens* to be more sensitive to the herbicides than *Pseudotsuga menziesii*, *Abies concolor*, *A. grandis*, *A. procera*, and *A. magnifica*. *Pinus ponderosa*, *P. contorta*, and *P. lambertiana* seemed to be less sensitive.

SALT

Picea sitchensis is less sensitive to ocean spray than *Tsuga heterophylla* or *Thuja plicata* on the west coast of Vancouver Island (Cordes 1973). Indeed, no other tree is more tolerant of ocean spray than *P. sitchensis* (Krajina 1970). When lower tolerance levels were compared, *Pinus ponderosa* was more salt-tolerant than *Pseudotsuga menziesii* (Monk and Wiebe 1961, Carpenter 1970).

SULFUR DIOXIDE

The sulfur dioxide produced by copper smelters and other large industrial installations has been damaging northwestern trees for many years. Mason (1915) ranked *Abies lasiocarpa* as the most easily killed Rocky Mountain species, fol-

Juniperus scopulorum, and *Pinus flexilis*. Scheffer and Hedgcock (1955) also rated *A. lasiocarpa* as most susceptible to SO_2 injury. They agreed with Mason's other observations, but added *Pinus ponderosa* var. *scopulorum* and ranked it more resistant than *Picea engelmannii* in Montana.

In the upper Columbia River Valley, Scheffer and Hedgcock found *Abies grandis* to be even more sulfur-dioxide-susceptible than *A. lasiocarpa*. They ranked *Thuja plicata* as slightly more resistant than *Abies lasiocarpa* in this locality but found *Pinus ponderosa* to be less SO_2 tolerant than *P. contorta*, *Larix occidentalis*, or *Picea engelmannii* (table 21). Farther west, on the British Columbia coast, *Tsuga heterophylla* is much more tolerant to sulfur dioxide than *Thuja plicata*, with *Abies amabilis* and *Picea sitchensis* resistance intermediate between these extremes (Miller and McBride 1975). *Tsuga mertensiana* and *Populus tremuloides* are sensitive to sulfur dioxide (U.S. Department of Agriculture 1973).

FLUORIDES

Picea glauca and the *Juniperus* species are tolerant of fluorides in the atmosphere (U.S. Department of Agriculture 1973). Produced by aluminum ore reduction plants and phosphate fertilizer factories, these fluorides cause more damage to *Pinus* species than to *Pseudotsuga menziesii* in Montana (Miller and McBride 1975). *P. menziesii* is damaged more than *Abies lasiocarpa*, *Thuja plicata*, and the *Picea* species. In Norway, Horntvedt and Robak (1975) also found *P. menziesii* to be damaged more than several other northwestern species. Their comparisons indicate the following fluoride ranking:

Tsuga heterophylla (least susceptible)
Abies procera
Picea engelmannii
Abies concolor
Pseudotsuga menziesii (most susceptible)

Table 21--Comparative air pollution tolerance of northwestern tree species[1]

Sulfur dioxide[2]	Fluorides[3]	Ozone[4]
Taxus brevifolia	*Tsuga heterophylla*	*Pinus lambertiana, Libocedrus decurrens*
Juniperus scopulorum	*Abies procera*	*Pinus ponderosa* var. *scopulorum, P. jeffreyi, P. attenuata, Pseudotsuga menziesii, Abies concolor*
Pinus ponderosa var. *scopulorum*	*Picea engelmannii*	*Pinus ponderosa, P. monticola, Abies magnifica*
Picea engelmannii	*Abies concolor*	
Larix occidentalis	*Pseudotsuga menziesii*	
Pinus contorta	*Pinus contorta*	
Pinus ponderosa	*Pinus ponderosa*	
Pinus monticola	*Pinus monticola*	
Pseudotsuga menziesii		
Tsuga heterophylla		
Abies amabilis, Picea sitchensis		
Thuja plicata		
Abies lasiocarpa		
Abies grandis		

[1] Resistant species are listed above susceptible ones. Species in the same group are not necessarily equal, but data are insufficient for species comparisons within groups.

[2] From Mason (1915), Scheffer and Hedgcock (1955), and Miller and McBride (1975).

[3] From Horntvedt and Robak (1975) and Miller and McBride (1975).

[4] From Miller and Millecan (1972) and Miller and McBride (1975).

OZONE

Ozone damage is serious in the forests near several urban centers in southern California, and it may become serious elsewhere as urban expansion continues. *Pinus ponderosa, P. monticola,* and *Abies magnifica* seem to be most sensitive to this pollution; *P. lambertiana* and *Libocedrus decurrens* are most tolerant (Miller and McBride 1975). *Sequoia sempervirens* and *Thuja plicata* also seem to tolerate ozone in the air (U.S. Department of Agriculture 1973). *Pinus ponderosa* var. *scopulorum, P. jeffreyi, P. attenuata, Pseudotsuga menziesii,* and *Abies concolor* appear to be

MISSING COMPARISONS

The species comparisons presented in this report are summarized in figure 1, with page numbers to provide access to relative species rankings and relationships. Figure 1 should serve as a useful index. In addition, it illustrates existing gaps in our knowledge of comparative autecological attributes. Some species (e.g., *Pseudotsuga menziesii, Tsuga heterophylla,* and *Pinus ponderosa*) have been compared with other species for most of the attributes listed. Others (e.g., *Chamaecyparis nootkatensis* and *Abies magnifica* var. *shastensis*) have been compared for less than peroxide to seeds as a substitute for lengthy stratification. *Pseudotsuga menziesii* and *Larix occidentalis* are benefitted more than *Abies lasiocarpa* by this treatment (Shearer and Tackle 1960). *P. menziesii* also benefits more than *Pinus lambertiana* or *P. ponderosa* when seeds are treated with hydrogen peroxide (Stein 1965).

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Picea engelmannii	*Abies concolor*	
Larix occidentalis	*Pseudotsuga menziesii*	
Pinus contorta	*Pinus contorta*	
Pinus ponderosa	*Pinus ponderosa*	
Pinus monticola	*Pinus monticola*	
Pseudotsuga menziesii		
Tsuga heterophylla		
Abies amabilis, Picea sitchensis		
Thuja plicata		
Abies lasiocarpa		
Abies grandis		

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Figure 1--A summary of autecological comparisons for the major northwestern tree species, with page numbers to indicate where the comparisons are found.

Autecological attributes	Major northwestern tree species1/																					
	AbAm	AbCo	AbGr	AbLa	AbMa-sh	AbPr	AlRu	ChLa	ChNo	LaOc	LiDe	PiEn	PiSi	PiCo	PiJe	PiLa	PiMo	PiPo	PsMe	ThPl	TsHe	TsMe
Air pollution tolerance	50,51	50,51	49,50,51	50,51		50,51				50,51	49,51	50,51	50,51	50,51	51	49,51	51	49,50,51	49,50,51	50,51	50,51	50
Animal damage		45	45					45			45		45			45		45	45,46	45,46	45,46	
Anthesis	25,26		25,26	25,26		25,26			25,26					26			26		25,26	25,26	25,26	25,26
Bark thickness		38	38	38		38,41			38	38		38	38	38			38,41	38	38,41	38,41	38,41	38
Cotyledon number	36	36	36	36	36	36		36	36	36	35,36	36	36	36	36	36	36	36	36	35,36	36	36
Crown density	40		37	37						37		37		37			37	37	37	37,40	37,40	
Crown length		37	37	35,37		37				35,37		35,37	37	37			35,37	35,37	35,37	37	37	37
Crown weight		35,36	36	36						35,36	35,36	36		35,36		36	35,36	35,36	35,36	36	36	
Crown width			37							37,40		37		37,40			37,40	37,40	37	37	37,40	
Decay resistance	48,49	48,49	48	48		48,49	48,49			48,49	48	48,49	48,49	48,49		48,49	48,49	48,49	48,49	48,49	48,49	48
Dense soil tolerance	39,45		45				45			39,45		45	39,45	39,45		39,45	39,45	39,45	39,44,45	39,45	39,45	
Drought tolerance	11,12	10,11,12	10,11,12	11,12	11,12	10		11,12		11,12	10,11	10,11	10,11	10,11	10,11	11,12	11,12	10,11	10,11,12	11,12	10,11,12	11,12
Epiphyte receptivity		38	38	38		38	38,42		38	38		38	38,42	38			38		38,42,43	38	38,43	38,42
Fire resistance		39	39,43	39,42		39				39,42,43	39	39,42	39,42,43	39,42		39	39	39	39,42,43	39,42,43	39,42	39
Foliage flammability		38	38	38		38				38		38	38	38			38	38	38	38	38	38
Frost tolerance	6,7	6,7	6,7	6,7	7		6,8	7	6	6	7	6,7	6,7,8	6,7	6,7	7	6,7	6,7	6,7,8	6,7,8	6,7,8	6,7
Germination rate	30	30,31	30,31		29,31	29,31					30,31	31,32			30,31	30,31,32	30,31,32	30,31	30,31,32		31	
Heat tolerance			8	8						8		8			8	8	8	8	8	8	8	
Herbicide tolerance		50	50			50	50						50	50		50		50	50		50	
Insect resistance	46,47	46,47	46,47	46,47	47	46,47		46,47		46,47	46,47	46,47	46	46	46,47	46,47	46,47	46,47	46,47	46,47	46,47	
Light intensity		5	5		5		6					6	5,6						5,6		5,6	
Litter fall	37						37						37	37,40			37	37	37,40	37,40	37	
Longevity	23	23	23	23		23	23	23	23	23	23	23	23	23		23	23	23	23	23	23	23
Moisture (excess)			12,13	12,13			12,13		13			12	12,13	12,13	13	12		12,13	12,13	12,13	12,13	13
Moisture (optimum)	14	14	14	15	14	14	14	15			13,14	15	14	15		14		13,14,15	13,14,15	14	14	14
Mycorrhizae	21	21	21	21	21	21	20,21	21	21	21	21	21	21	21	21	21	21	20,21	20,21	21	20,21	21

Autecological attributes	AbAm	AbCo	AbGr	AbLa	AbMa-sh	AbPr	AlRu	ChLa	ChNo	LaOc	LiDe	PiEn	PiSi	PiCo	PiJe	PiLa	PiMo	PiPo	PsMe	ThPl	TsHe	TsMe
Needle density							35						35	35			35		35		35	
Needle longevity	36		36										36	36			36	36	36		35,36	
Needle volume			36										36	36			36		36		36	
Needle weight	36		36										36	36			36		36		36	
Nutrient concentrations	15,16, 17		15,16	15,16, 17	16		16,17	15,17		16,17		15,16, 17	15,16, 17	16,17			16	16,17	15,16, 17	15,16, 17	15,16, 17	
Nutrient deficiencies	19	19	19	19	19				18		19	18,19	17,18, 19	19	19	19	17,18, 19	17,18 19	17,18, 19	17,18 19	18,19	19
Nutrient excesses													19	19					19	19	19	
Root growth rate			22	22						22,23	22,23	22	22,23	22,23		22,23	22,23	22,23	22,23	22,23	22,23	
Rooting depth	43		39,43	43						39	39,43			43		39,43	39	39,43	39,43	39,43	39,43	
Sapwood thickness						40				38		38		38				38,40	38,40	38		
Seed bearing age	26	26		25	26	26	26	26		26		25	26	26	26	26	26	26	26	26	26	26
Seedbeds	34		33,34	33,34			33,34			33,34	32	33,34	32,33, 34	33,34		32	33	33,34	32,33, 34	32,33, 34	32,33, 34	
Seed crop frequency	27		27	27						27,28		27,28	28	27,28			27,28	27,28	27	27,28	27,28	27
Seed crop size	27,28	27,28	28		28	28		27,28	27	27,28	28	28	27	27	27	27,28	28	27,28	27,28	27	27,28	28
Seed dissemination	25,26, 27	26	25,26, 27	26,27	26	25,26, 27		26	26	25,26	26	26	25,26	26	26	26	25,26	26	25,26, 27	25,26, 27	25,26, 27	
Seed flight	29,30	30	30			29					30	29	29,30	30	30	29,30	29	29,30	29,30	29,30	29,30	
Seed longevity		31	31	31		31		31		31	31	31	31	31	31	31	31	31	31	31	31	31
Seed stratification	31,32	31	31,32	31	31	31,32		31				31,32	31,32	31	31	31,32	31,32	31,32	31,32	31,32	31,32	
Seed weight	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30
Shade tolerance	3,4	3,4	3,4	3,4	3,4, 5	3,4, 5	3,5	3,5	3,4	3,5	3,5	3,4, 5	3,4	3,4, 5		3,4, 5	3,4, 5	3,5	3,4, 5	3,4	3,4, 5	3,4
Shoot growth period	23,24	23,24	23,24	24		23,24		23,24			23,24		23,24	23,24	23,24	23,24	24	23,24	23,24	23,24	23,24	24
Size	23	23,24	23	23		23	23,24	23	23	23	23,24	23	23,24	23		23	23	23,24	23,24	23,24	23,24	23
Slash flammability			41,42							41,42		41,42		41,42			41,42	41,42	41,42	41,42	41,42	
Snow damage	39,45	39,45			39,45	39,45									39,45	39,45	39,45	39,45	39,45		39,45	39,45
Specific gravity	37,40	37,40	37,38 40	37		37,40	37	37		37,38, 40	37	37,40	37	37,38	37	37	37	37,40	37,38, 40	37,40	37	37
Temperature (mean)	9		9	8,9	9	9					8,9	8	9	8,9		8,9		8,9	8,9	9	8,9	9
Windthrow resistance	39,44					44				44			39,44					44	39,44	39,44	39,44	

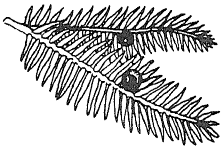
1/ Species names are abbreviated as follows: AbAm = *Abies amabilis*; AbCo = *Abies concolor*; AbGr = *Abies grandis*; AbLa = *Abies lasiocarpa*; AbMa-sh = *Abies magnifica* var. *shastensis*; AbPr = *Abies procera*; AlRu = *Alnus rubra*; ChLa = *Chamaecyparis lawsoniana*; ChNo = *Chamaecyparis nootkatensis*; LaOc = *Larix occidentalis*; LiDe = *Libocedrus decurrens*; PiEn = *Picea engelmannii*; PiSi = *Picea sitchensis*; PiCo = *Pinus contorta*; PiJe = *Pinus jeffreyi*; PiLa = *Pinus lambertiana*; PiMo = *Pinus monticola*; PiPo = *Pinus ponderosa*; PsMe = *Pseudotsuga menziesii*; ThPl = *Thuja plicata*; TsHe = *Tsuga heterophylla*; TsMe = *Tsuga mertensiana*.

As one would expect, widespread species have been compared more than those with limited ranges. *Chamaecyparis lawsoniana* comparisons are particularly scarce. As. *C. lawsoniana* is a valuable species seriously threatened by disease, its autecological attributes probably should be related to those of other species. Such autecological comparisons might help pathology researchers and provide information about suitable substitutes if *C. lawsoniana*'s ecological niche must be occupied by other species.

Pinus jeffreyi appears to be another species that seldom has been compared because of its limited range. It may resemble *P. ponderosa* in some cases where blanks appear in figure 1, but probably has several unique attributes that are not matched in other species. Nutrient concentrations and mean temperature comparisons seem particularly worthy of investigation in *P. jeffreyi*.

Limited range probably does not account for the surprising lack of *Alnus rubra* comparisons. Its low commercial value may be responsible. Whatever the reason, *A. rubra* comparisons should be neglected no longer. Root growth rate and rooting depth relationships seem particularly pertinent in light of *A. rubra*'s nitrogen fixing characteristics (Tarrant and Miller 1963, Bollen et al. 1967, Franklin et al. 1968, and Tarrant et al. 1969). Its tolerance of nutrient deficiencies also should be compared with associated species.

Associated species probably should be compared in as many ways as possible, wherever they grow. Considerable amounts of work remain to be done if this is to be accomplished for the autecological attributes listed here. Comparative crown, needle, and root characteristics, litter fall, slash flammability, and windthrow resistance are all sparsely represented in figure 1.



UNKNOWN ATTRIBUTES

The autecological attributes compared in this report are somewhat subjective. They represent attempts to delineate and define discrete variables in the non-discrete continuum of interacting characteristics that define the nature and properties of northwestern tree species as we know them. Others might use somewhat different categories or discuss these attributes under different headings. Nevertheless, the attributes do exist as such, and most have been compared in this report--however one wishes to categorize and name them.

Some attributes have not been compared, however, for they seem to be absent from the literature. As comparable information is lacking, these attributes constitute unknowns...not just for one or two but for most northwestern tree species.

Most northwestern tree species grow in mixed stands, where they compete with other species. Relative ability to compete constitutes an autecological unknown. Unfortunately, it is an unknown that must be qualified by knowing where the competition will occur and in what environment. Comparative competitive abilities probably will remain unknown until they are determined in various environments throughout the natural ranges of the species involved.

Potential species ranges constitute another unknown autecological attribute. Where would each species occur if it possessed a capacity for worldwide distribution and was not limited by competition with other species? A complete knowledge of all other attributes, for all species, may be a prerequisite to answering this question. It probably will remain unanswered for the forseeable future.

Fortunately, several other attributes are less likely to remain unknown. Study of mycorrhizal relationships is now being accelerated, and detailed comparisons among northwestern species should be available in a few more years. Although the fungus-host relationships may be rather specific, it should soon be possible to rate northwestern tree species in terms of mycorrhizae dependence and numbers of fungi involved.

Genetic variability and gene-pool characteristics also are being studied for several northwestern tree species. Genetic plasticity may vary greatly among species, and some gene pools probably are larger and more complex than others. Better understanding of these presently unknown genetic attributes may permit species comparisons that are impossible today. It also should improve all present species ratings by facilitating evaluation of within-and-among species variations.

Although coniferous forests selectively filter light (Atzet and Waring 1970), among-species comparisons of light filtering properties and foliage albedo were not found in the literature--apparently because they are little known for northwestern tree species. Like many of the comparisons missing for individual species, these attributes probably will be recorded and compared as the needed research is accomplished.

RESEARCH NEEDS

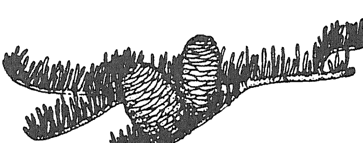
Additional research is needed to supply the missing information indicated by blank spaces in figure 1 and to describe the unknown attributes discussed above. More than this is needed, however, even for the filled spaces in figure 1 and for well-known autecological attributes. Many of the comparisons cited here were based upon observations rather than measurements, and most occurred under conditions that could have influenced the results by introducing imperceptible extraneous influences. Quantification and refinement of these comparisons through rigorous experimental procedures carried out under controlled conditions should result in more consistent, reliable conclusions.

Quantitative comparison of photosynthetic activity under various light conditions has been accomplished for few species. It should be done for all, at several ambient temperatures. Photoperiodic responses also relative light requirements for strobilus formation, anthesis, and dormancy. Again, several ambient temperatures should be used to investigate the light, temperature, and species interactions.

Species-environment interactions probably are as important as specie attributes themselves when growth i being compared in the field. These interactions should be studied carefully by establishing replicated species trials in many different field environments. Wherever possi these field environments should be categorized by quantitative measurements. They should always be classified or described in ways that allow comparison and contrast with other environments.

Growth comparisons in the field often require long-term experiments that may exceed the professional life span of any single researcher. Comparisons of germination rates, stratification requirements, and optimal germination temperatures do not have this inherent disadvantage. Environmental interaction are also important in these short-term comparisons, however, and they should be accomplished in carefully designed experiments that will result in usable interaction data.

Finally, it should be emphasized that two or more species should be tested together and compared whenever possible in autecological experimentation. Even the most well-designed experiment, carried out under highly controlled conditions, is somewhat unique. Exactly identical conditions are impossible to attain again, regardless of the precautions taken. Comparative data involving more than one species may allow further extrapolation of experimental results than that which is possible with a single species, and wider inferences often may be made. Relative comparisons tend to be more widely applicable than absolute, isolated results.



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